

# A Systematic Review of the Hydrobiid Snails (Gastropoda: Rissooidea) of the Great Basin, Western United States. Part I. Genus *Pyrgulopsis*

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**Abstract.** A recently completed field survey of springs throughout the Great Basin yielded collections of hydrobiid snails from more than 500 sites, and revealed a wealth of undescribed diversity of these small gastropods. In this, the first of a two-part taxonomic series treating this material, 58 new species of *Pyrgulopsis* Call & Pilsbry, 1886, are described; and new records are provided for 10 previously described members of this genus. Assignment of these novelties to *Pyrgulopsis* is done with the acknowledgement that this large genus, as currently constituted, is probably not monophyletic, but a more refined classification of these snails reflecting evolutionary relationships must await preparation of a phylogenetic analysis, which is beyond the scope of this work. *Pyrgulopsis* occur in a variety of spring-fed water bodies in the Great Basin, including brackish and/or thermal habitats. Although a few species are widespread in the region, local endemism is prevalent and 22 of the new species are known only from single localities. Several areas contain concentrations of locally endemic snails which may represent species flocks, notably Duckwater Valley (seven species) and southern Steptoe Valley (five species). This fauna is largely distributed in an allopatric fashion, although a few springs harbor two or three species. Most of the springs inhabited by hydrobiids in the region are small, fishless, and have been ignored by state and federal land management agencies. However, many of these sites are degraded by livestock grazing, water withdrawal, and other activities and will require protection in order to conserve snails and other native aquatic biota. Two of the novelties described herein have become extinct during the past two decades.

... the western states appear to present a set of conditions that should encourage isolation and speciation, especially in certain taxa containing macroscopic forms and the West should theoretically have a unique population of freshwater invertebrates. ... Indeed, there is already evidence to show that the western aquatic invertebrate fauna is much richer and more varied than is indicated in the literature. (Pennak, 1958:224)

## INTRODUCTION

Pennak's assertion that the aquatic invertebrate fauna of the western United States is undersampled was accompanied by a plea for colleagues to pursue more field, laboratory, and zoogeographic work in the region and publish the results of these endeavors. Although his prediction has been affirmed by the unabated publication of new taxa from the region over the past 28 years (e.g., Holsinger, 1974; Holsinger & Longley, 1980; Taylor, 1987), large areas in the West still have not been comprehensively surveyed and various aquatic invertebrate groups remain poorly known. Among the latter are the ubiquitous, locally abundant (Noel, 1954), small freshwater gastropods of the family Hydrobiidae, which total about 100 described species in the West. These snails are tightly linked with their aquatic habitat and often are endemic to single water bodies (particularly springs) or local drainage systems, features which render the group eminently suitable for zoogeographic inquiry (Taylor & Bright, 1987) and also thrust them into prominence with respect to ongoing efforts to conserve and manage western aquat-

ic ecosystems. Much of this snail fauna now is imperiled—although a few species have been added to the Federal List of Threatened and Endangered Wildlife, a more telling indication of the status of the fauna is the fact that until recently, when the U.S. Fish and Wildlife Service discontinued designation of Category 2 species as candidates (USDI, 1996), most of these snails were candidates for addition to this list (e.g., USDI, 1994).

Although western hydrobiids are poorly known, the fauna of the Great Basin, in particular, has been neglected. This huge (500,000 km<sup>2</sup>), remote and relatively rugged region is composed of more than 100, typically isolated, drainage basins (Mifflin, 1988:fig. 3) that were variously integrated during the wetter or pluvial period of the Late Quaternary (11,000–13,000 ybp) when many large lakes or wetlands were present (Figure 1). Although about 40 nominal species of hydrobiids have been recorded from the region, the group has not figured prominently in the few faunal surveys of the region (e.g., Brues, 1928, 1932), and published collections are from relatively few, widely scattered locales. Field coverage has been extremely uneven as, for instance, the Great

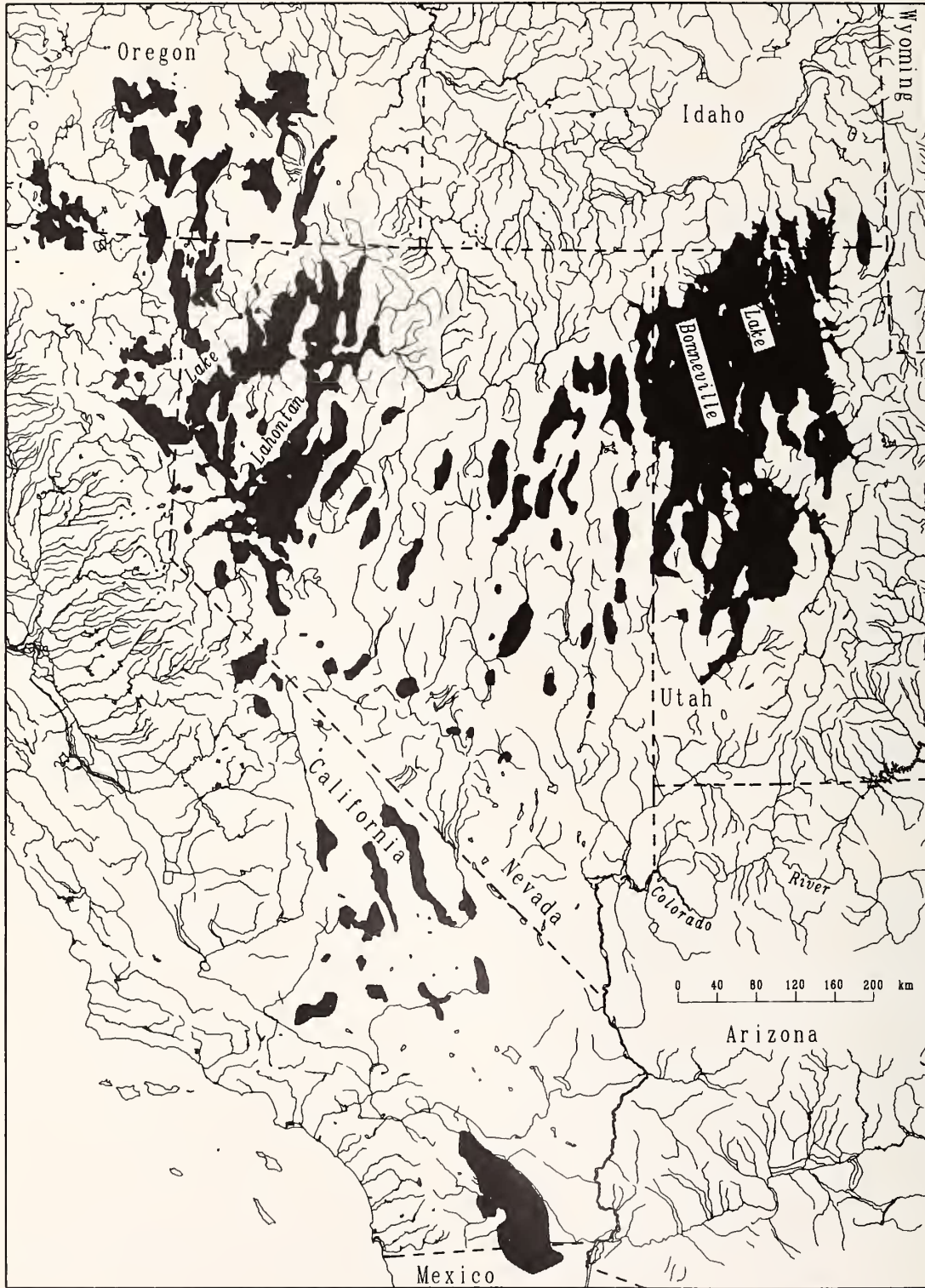


Figure 1

Map showing pluvial lakes (black) of the Great Basin superimposed on modern drainage (lake distribution from Mifflin & Wheat, 1979; King, 1982; Currey et al., 1983; Williams & Bedinger, 1984).

Basin of Utah was relatively well surveyed by Chamberlin, Jones, and other workers, while Nevada scarcely has been touched. However, the literature also provides indications that much fauna remains to be described (e.g., Deacon et al., 1980; J. E. Williams et al., 1985; Taylor & Bright, 1987:241). The paucity of collecting activity has important biogeographic implications as, for instance, the widely cited "fish hook" pattern, a distributional track attributed to various mollusks (and fishes) and extending from the eastern Bonneville Basin via the middle Snake River and western Lahontan basin to the Death Valley system (Taylor, 1960:figs. 1–3; Taylor, 1966a:fig. 7; Smith, 1981) may reflect inadequate sampling in the Great Basin of northern Nevada. Furthermore, most of the previous work on this fauna was published prior to the advent of modern approaches to gastropod systematics, and consisted of descriptions of single species based on empty shells. Many shell characters have proven unreliable, and hence these treatments are of limited utility today. The minimal attention paid to the hydrobiid snails of the Great Basin may be partly attributable to an impression that the desert basins of this region are largely devoid of aquatic biota: note that a large, fishless portion of south-central Nevada was named the "area of sterile basins" by Hubbs & Miller (1948:45).

There is an urgent need for discovery and documentation of these snails, as the typical habitats of Great Basin hydrobiids, very small springs that are often less than 1 m wide and 1 cm deep, are fragile, unprotected, and prone to extreme degradation owing to water development in the region, particularly livestock grazing. To fulfill this need and generate a biogeographic database I began field survey in 1985 of the Death Valley system, a large pluvial drainage in southwestern Nevada and southeastern California. Completion of this survey led to the description of 19 new species of hydrobiids from the region (Hershler & Sada, 1987; Hershler, 1989; Hershler & Pratt, 1990). Field survey then shifted to the remaining portions of the Great Basin in California, which led to discovery of an additional three new species (Hershler, 1995). From 1991–1995, a survey of the rest of the hydrographic Great Basin<sup>1</sup> was conducted. This included portions of Idaho, Nevada (exclusive of previously visited portions of the Death Valley system), Oregon, Utah, and Wyoming. Drainages of the Colorado River and Snake River in Nevada also were visited. During the survey more than 2000 sites were visited. Hydrobiid snails were collected from more than 500 springs, and many new taxa were discovered. The purpose of this paper, the first of a two-part taxonomic series, is to describe the new material of *Pyrgulopsis* Call & Pilsbry, 1886, the largest genus of hydrobiids in North America. In a recent review (Her-

shler, 1994), I recognized 65 Recent species in *Pyrgulopsis*; eight more new species have since been introduced (Hershler, 1995; Thompson, 1995). Herein an additional 58 new species are described, as are numerous new records for 10 previously described members of this genus.

Novelties described herein are allocated to *Pyrgulopsis* in the broad sense utilized by Hershler (1994). Note that a preliminary phylogenetic hypothesis for species in this genus (Hershler, 1994:fig. 31) permitted recognition of several well-supported clades within this group, which may be better treated as separate genera in the future. (Monophyly of *Pyrgulopsis* was not well tested as only a single outgroup was used.) Several additional morphologically cohesive groups are described herein, but allocation of these to new genera is tabled until a more comprehensive phylogenetic review of *Pyrgulopsis* is prepared. Fauna described herein includes not only several distinct, well-delineated groups, some of which may represent local "species flocks" (e.g., in Railroad and Step-toe Valleys), but also a large number of relatively similar yet geographically scattered species of uncertain affinities. Although the latter are contrasted principally on the basis of penial form and ornament, the reader should be aware that characters derived from these features are probably subject to homoplasy and may be misleading with regard to phylogenetic signal. Thus, for instance, it is difficult to confidently ascertain whether some of the new species modestly endowed with glandular ornament on the penis are allied with snails having similar penes or, alternatively, should be interpreted as reduced forms derived from either of two regionally widespread species, *P. gibba* Hershler, 1995, and *P. kolobensis* (Taylor, 1987). Given the large number of species and relatively small number of characters used in the descriptions, it will be difficult to unravel the phylogenetic relationships among these taxa using morphological criteria alone. In any event, such an analysis is beyond the scope of this paper, as it will require additional study of the many other congeners (encompassing characters not utilized in my earlier review) as well as re-evaluation of concepts of character discrimination and state coding based on information derived from the current study.

## MATERIALS AND METHODS

This work was principally based on study of material (dry shell and anatomical components) collected during the recent field survey (and now deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.), as other museum material from the region is scarce and almost always of empty shell, which usually cannot be confidently identified to species in this group. Identification of springs to be surveyed was facilitated by study of United States Geological Survey topographic maps (1:100,000 scale) and communications from various colleagues (see Acknowledgments). Mate-

<sup>1</sup> This restricts the Great Basin to the region characterized by internal drainage. Other definitions (physiographic or floristic) outline slightly different regions (see D'Azevedo, 1986:fig. 2).

Table 1

Selected shell parameters for new species of *Pyrgulopsis*. Data expressed as mean with standard deviation given below. Measurements are given in mm.  $n$  = number of specimens,  $\mu$  = mean,  $s$  = standard deviation, SH = shell height, SW = shell width, HBW = height of body whorl, WBW = width of body whorl, AH = aperture height, AW = aperture width, SS = shell width/shell height, WH = number of shell whorls. In lots marked with an asterisk, the majority of specimens measured had eroded apices.

		SH	SW	HBW	WBW	AH	AW	SS	WH
<i>P. fausta</i>									
USNM 874757	$\mu$	1.56	1.38	1.33	1.11	0.91	0.76	0.88	3.03
$n = 15$	$s$	0.07	0.05	0.05	0.03	0.04	0.05	0.03	0.13
<i>P. deaconi</i>									
USNM 874454	$\mu$	1.78	1.49	1.52	1.25	0.98	0.84	0.84	3.18
$n = 15$	$s$	0.09	0.07	0.07	0.06	0.06	0.05	0.03	0.11
<i>P. coloradensis</i>									
USNM 854621	$\mu$	1.31	1.13	1.14	0.89	0.74	0.65	0.86	3.17
$n = 15$	$s$	0.13	0.08	0.08	0.05	0.05	0.03	0.05	0.25
<i>P. montana</i>									
USNM 874686	$\mu$	2.38	1.79	1.86	1.56	1.17	0.93	0.75	3.51
$n = 15$	$s$	0.21	0.11	0.15	0.11	0.08	0.09	0.03	0.26
<i>P. hubbsi</i>									
*USNM 873415	$\mu$	3.14	2.83	2.88	2.22	2.10	1.51	0.90	3.51
$n = 15$	$s$	0.25	0.23	0.22	0.18	0.13	0.19	0.03	0.11
USNM 873405	$\mu$	2.82	2.47	2.54	1.89	1.78	1.40	0.88	3.51
$n = 15$	$s$	0.21	0.13	0.18	0.12	0.12	0.08	0.03	0.18
<i>P. sathos</i>									
USNM 874464	$\mu$	3.47	2.49	2.67	2.15	1.56	1.32	0.72	4.43
$n = 15$	$s$	0.17	0.14	0.16	0.10	0.10	0.07	0.03	0.20
USNM 873198	$\mu$	4.19	3.17	2.97	2.74	1.89	1.54	0.76	4.85
$n = 15$	$s$	0.18	0.18	0.13	0.15	0.11	0.10	0.03	0.18
USNM 874663	$\mu$	1.57	1.35	1.19	1.14	0.81	0.66	0.86	3.45
$n = 15$	$s$	0.15	0.09	0.10	0.07	0.06	0.06	0.04	0.22
USNM 883852	$\mu$	4.03	3.02	2.94	2.56	1.96	1.52	0.75	4.66
$n = 15$	$s$	0.32	0.17	0.21	0.14	0.11	0.13	0.04	0.20
<i>P. breviloba</i>									
USNM 883846	$\mu$	1.67	1.41	1.46	1.10	0.96	0.80	0.85	3.32
$n = 10$	$s$	0.12	0.12	0.12	0.08	0.09	0.06	0.05	0.12
USNM 874671	$\mu$	1.28	1.15	1.09	0.92	0.75	0.60	0.87	3.00
$n = 15$	$s$	0.07	0.05	0.07	0.05	0.03	0.04	0.03	0.13
USNM 873188	$\mu$	1.69	1.51	1.46	1.11	1.03	0.77	0.89	3.55
$n = 15$	$s$	0.11	0.13	0.09	0.08	0.07	0.05	0.05	0.14
<i>P. lata</i>									
USNM 873167	$\mu$	1.95	1.42	1.57	1.22	0.93	0.69	0.73	4.08
$n = 15$	$s$	0.08	0.10	0.07	0.06	0.06	0.10	0.04	0.12
<i>P. gracilis</i>									
*USNM 873158	$\mu$	1.71	1.47	1.36	1.26	0.98	0.70	0.86	2.98
$n = 12$	$s$	0.08	0.08	0.08	0.06	0.06	0.07	0.04	0.55
<i>P. marcida</i>									
USNM 873154	$\mu$	3.41	2.63	2.48	2.18	1.64	1.31	0.77	4.15
$n = 15$	$s$	0.17	0.15	0.16	0.11	0.09	0.11	0.03	0.21
USNM 873170	$\mu$	2.73	1.94	2.06	1.68	1.26	0.98	0.71	4.22
$n = 15$	$s$	0.15	0.08	0.10	0.08	0.04	0.05	0.03	0.23
*USNM 874672	$\mu$	1.79	1.41	1.47	1.20	0.98	0.77	0.79	3.52
$n = 15$	$s$	0.13	0.07	0.10	0.06	0.08	0.05	0.04	0.15
USNM 874682	$\mu$	3.12	2.45	2.39	2.09	1.59	1.25	0.77	3.75
$n = 15$	$s$	0.22	0.18	0.14	0.11	0.10	0.09	0.03	0.16

Table 1  
Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
<i>P. turbatrix</i>									
USNM 883978	$\mu$	3.08	1.96	2.22	1.65	1.26	1.15	0.64	4.45
<i>n</i> = 15	s	0.15	0.07	0.10	0.06	0.07	0.05	0.03	0.17
USNM 857936	$\mu$	2.28	1.60	1.77	1.38	1.06	0.94	0.70	3.82
<i>n</i> = 15	s	0.11	0.05	0.07	0.04	0.05	0.04	0.03	0.15
USNM 883550	$\mu$	3.22	2.00	2.20	1.75	1.24	1.04	0.62	4.67
<i>n</i> = 13	s	0.20	0.09	0.11	0.08	0.06	0.06	0.03	0.19
USNM 883981	$\mu$	2.51	1.80	1.88	1.52	1.12	1.01	0.72	4.00
<i>n</i> = 15	s	0.15	0.13	0.11	0.07	0.09	0.06	0.02	0.21
<i>P. sterilis</i>									
USNM 874876	$\mu$	3.51	2.41	2.49	2.06	1.56	1.26	0.69	4.30
<i>n</i> = 15	s	0.19	0.09	0.15	0.07	0.10	0.06	0.03	0.22
USNM 874679	$\mu$	2.52	2.00	2.05	1.60	1.30	1.15	0.80	3.43
<i>n</i> = 15	s	0.16	0.11	0.10	0.11	0.09	0.06	0.02	0.18
<i>P. ruinosa</i>									
USNM 873407	$\mu$	2.91	2.08	2.25	1.83	1.35	1.05	0.72	4.02
<i>n</i> = 15	s	0.19	0.14	0.14	0.11	0.10	0.08	0.05	0.22
<i>P. sublata</i>									
USNM 874681	$\mu$	2.42	1.73	1.81	1.56	1.12	0.91	0.72	4.18
<i>n</i> = 15	s	0.18	0.14	0.12	0.12	0.08	0.08	0.03	0.20
<i>P. lockensis</i>									
USNM 874779	$\mu$	1.79	1.53	1.37	1.27	0.89	0.80	0.86	3.50
<i>n</i> = 15	s	0.08	0.05	0.05	0.04	0.04	0.03	0.03	0.21
<i>P. papillata</i>									
USNM 873185	$\mu$	2.04	1.76	1.62	1.45	1.10	0.99	0.87	3.43
<i>n</i> = 15	s	0.10	0.06	0.07	0.06	0.06	0.05	0.04	0.15
<i>P. carinata</i>									
USNM 883975	$\mu$	2.10	1.77	1.67	1.47	1.09	0.91	0.85	3.71
<i>n</i> = 12	s	0.22	0.14	0.16	0.11	0.07	0.09	0.03	0.21
<i>P. aloba</i>									
*USNM 883847	$\mu$	1.18	1.04	1.03	0.86	0.68	0.57	0.89	2.42
<i>n</i> = 12	s	0.08	0.06	0.07	0.05	0.06	0.04	0.05	0.27
USNM 873187	$\mu$	1.30	1.19	1.14	0.97	0.79	0.65	0.92	3.10
<i>n</i> = 15	s	0.16	0.13	0.12	0.11	0.09	0.07	0.03	0.18
<i>P. villacampae</i>									
USNM 873191	$\mu$	2.82	2.52	2.47	2.00	1.62	1.53	0.90	3.37
<i>n</i> = 15	s	0.14	0.10	0.15	0.07	0.10	0.09	0.04	0.16
USNM 883938	$\mu$	3.37	2.87	2.78	2.27	1.86	1.69	0.85	3.81
<i>n</i> = 12	s	0.21	0.14	0.20	0.10	0.13	0.11	0.03	0.19
<i>P. anatina</i>									
USNM 883848	$\mu$	2.66	2.01	1.95	1.71	1.28	1.04	0.76	4.00
<i>n</i> = 15	s	0.13	0.11	0.10	0.07	0.07	0.06	0.03	0.19
<i>P. planulata</i>									
*USNM 892023	$\mu$	1.30	1.29	1.26	1.15	0.80	0.72	1.00	2.01
<i>n</i> = 15	s	0.06	0.08	0.07	0.06	0.06	0.05	0.05	0.24
<i>P. sulcata</i>									
USNM 874326	$\mu$	1.31	1.11	1.05	0.96	0.71	0.56	0.85	3.80
<i>n</i> = 15	s	0.06	0.03	0.04	0.04	0.03	0.03	0.03	0.17
<i>P. orbiculata</i>									
USNM 873196	$\mu$	1.28	1.13	1.08	0.97	0.70	0.60	0.88	3.53
<i>n</i> = 15	s	0.05	0.04	0.04	0.02	0.02	0.03	0.04	0.19
<i>P. neritella</i>									
*USNM 883932	$\mu$	1.45	1.35	1.40	1.03	0.99	0.91	0.93	2.30
<i>n</i> = 15	s	0.08	0.05	0.11	0.05	0.06	0.06	0.05	0.40

Table 1  
Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
*USNM 883936	$\mu$	1.33	1.08	1.32	1.05	0.86	0.75	0.82	1.62
<i>n</i> = 15	s	0.08	0.05	0.08	0.05	0.06	0.06	0.03	0.21
<i>P. landyei</i>									
*USNM 892014	$\mu$	1.41	1.25	1.25	1.12	0.78	0.68	0.89	3.02
<i>n</i> = 15	s	0.08	0.07	0.06	0.04	0.06	0.05	0.03	0.35
<i>P. serrata</i>									
USNM 874314	$\mu$	2.22	1.73	1.75	1.49	1.05	0.93	0.78	3.73
<i>n</i> = 15	s	0.11	0.09	0.09	0.06	0.06	0.05	0.05	0.18
*USNM 874312	$\mu$	3.54	2.30	2.33	2.09	1.35	1.15	0.65	4.48
<i>n</i> = 13	s	0.30	0.13	0.14	0.12	0.09	0.07	0.04	0.45
USNM 874318	$\mu$	2.32	1.73	1.78	1.49	1.09	0.96	0.75	3.93
<i>n</i> = 15	s	0.15	0.10	0.10	0.08	0.09	0.06	0.05	0.15
<i>P. cruciglans</i>									
USNM 874285	$\mu$	1.78	1.40	1.41	1.19	0.89	0.75	0.79	3.80
<i>n</i> = 15	s	0.10	0.04	0.06	0.05	0.03	0.03	0.03	0.17
USNM 874327	$\mu$	2.39	1.88	1.93	1.57	1.20	1.06	0.79	3.87
<i>n</i> = 15	s	0.13	0.08	0.10	0.08	0.06	0.05	0.04	0.18
USNM 874331	$\mu$	2.33	1.84	1.83	1.53	1.13	0.98	0.79	3.90
<i>n</i> = 15	s	0.13	0.08	0.08	0.06	0.07	0.06	0.04	0.16
USNM 874335	$\mu$	2.33	1.86	1.85	1.57	1.20	0.98	0.80	3.92
<i>n</i> = 15	s	0.19	0.13	0.13	0.11	0.08	0.07	0.04	0.15
<i>P. dixensis</i>									
USNM 874391	$\mu$	1.78	0.91	1.08	0.86	0.62	0.50	0.52	4.82
<i>n</i> = 15	s	0.10	0.03	0.06	0.04	0.04	0.03	0.02	0.24
<i>P. aurata</i>									
USNM 874393	$\mu$	2.69	2.14	2.19	1.70	1.37	1.18	0.80	3.92
<i>n</i> = 15	s	0.13	0.09	0.11	0.07	0.08	0.06	0.02	0.18
<i>P. longiglans</i>									
USNM 873409	$\mu$	2.41	1.81	1.92	1.52	1.27	1.02	0.76	3.90
<i>n</i> = 15	s	0.08	0.05	0.06	0.04	0.03	0.03	0.03	0.13
USNM 874288	$\mu$	1.54	1.27	1.27	1.06	0.85	0.62	0.82	3.45
<i>n</i> = 15	s	0.10	0.06	0.07	0.06	0.04	0.03	0.02	0.17
USNM 883486	$\mu$	1.97	1.58	1.57	1.32	1.03	0.77	0.80	3.93
<i>n</i> = 15	s	0.08	0.09	0.06	0.05	0.05	0.05	0.03	0.11
USNM 874293	$\mu$	1.93	1.55	1.60	1.27	1.10	0.80	0.80	3.67
<i>n</i> = 15	s	0.16	0.10	0.11	0.07	0.08	0.06	0.04	0.18
USNM 874396	$\mu$	2.10	1.59	1.69	1.34	1.12	0.85	0.76	3.87
<i>n</i> = 15	s	0.10	0.06	0.08	0.04	0.04	0.05	0.03	0.16
USNM 874904	$\mu$	1.79	1.41	1.44	1.18	0.96	0.69	0.79	3.82
<i>n</i> = 15	s	0.11	0.06	0.08	0.05	0.05	0.03	0.03	0.20
<i>P. militaris</i>									
USNM 873203	$\mu$	1.44	1.23	1.23	0.96	0.83	0.65	0.85	3.52
<i>n</i> = 15	s	0.08	0.05	0.06	0.04	0.05	0.04	0.03	0.11
USNM 883921	$\mu$	1.75	1.46	1.46	1.17	0.93	0.76	0.83	3.48
<i>n</i> = 15	s	0.10	0.06	0.08	0.05	0.05	0.03	0.04	0.15
<i>P. umbilicata</i>									
USNM 873208	$\mu$	2.13	1.74	1.71	1.49	1.05	0.89	0.82	3.80
<i>n</i> = 15	s	0.08	0.07	0.07	0.07	0.05	0.05	0.02	0.10
USNM 873202	$\mu$	1.87	1.59	1.53	1.32	1.02	0.82	0.85	3.72
<i>n</i> = 15	s	0.11	0.08	0.08	0.06	0.05	0.04	0.03	0.16
<i>P. limaria</i>									
USNM 873232	$\mu$	1.55	1.41	1.31	1.14	0.90	0.71	0.91	3.45
<i>n</i> = 15	s	0.10	0.06	0.08	0.06	0.04	0.04	0.04	0.14

Table 1  
Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
<i>P. notidicola</i>									
USNM 873215	$\mu$	2.22	1.83	1.95	1.45	1.25	1.07	0.82	3.47
<i>n</i> = 15	s	0.09	0.08	0.08	0.06	0.04	0.04	0.04	0.14
USNM 874286	$\mu$	1.56	1.40	1.37	1.05	0.93	0.79	0.89	3.18
<i>n</i> = 15	s	0.13	0.10	0.11	0.07	0.06	0.06	0.03	0.15
USNM 874294	$\mu$	1.78	1.50	1.57	1.20	0.99	0.88	0.84	3.30
<i>n</i> = 15	s	0.07	0.07	0.07	0.05	0.05	0.06	0.03	0.10
<i>P. vinyardi</i>									
USNM 874740	$\mu$	1.72	1.45	1.54	1.17	0.98	0.86	0.84	3.25
<i>n</i> = 14	s	0.11	0.08	0.09	0.06	0.05	0.06	0.04	0.14
<i>P. imperialis</i>									
USNM 874207	$\mu$	1.53	1.12	1.21	0.95	0.76	0.58	0.73	3.43
<i>n</i> = 15	s	0.07	0.06	0.05	0.04	0.03	0.04	0.04	0.18
USNM 874211	$\mu$	1.59	1.17	1.26	1.00	0.78	0.60	0.74	3.45
<i>n</i> = 15	s	0.09	0.07	0.06	0.04	0.04	0.04	0.04	0.17
<i>P. sadai</i>									
USNM 874397	$\mu$	2.68	2.07	2.17	1.75	1.37	1.08	0.77	4.17
<i>n</i> = 15	s	0.09	0.09	0.08	0.06	0.05	0.08	0.02	0.11
USNM 874208	$\mu$	2.31	1.86	1.87	1.57	1.21	0.98	0.81	3.88
<i>n</i> = 15	s	0.13	0.08	0.11	0.09	0.05	0.06	0.03	0.13
USNM 874388	$\mu$	2.20	1.84	1.84	1.56	1.20	0.99	0.84	3.58
<i>n</i> = 15	s	0.17	0.11	0.12	0.09	0.07	0.06	0.02	0.20
USNM 874392	$\mu$	2.38	1.78	1.85	1.55	1.14	0.99	0.75	3.87
<i>n</i> = 15	s	0.19	0.10	0.12	0.09	0.07	0.06	0.03	0.19
USNM 883900	$\mu$	2.92	2.16	2.25	1.91	1.36	1.12	0.74	4.13
<i>n</i> = 15	s	0.16	0.07	0.09	0.07	0.04	0.04	0.04	0.13
<i>P. augustae</i>									
USNM 874402	$\mu$	2.32	1.45	1.71	1.26	1.07	0.77	0.63	4.25
<i>n</i> = 14	s	0.10	0.07	0.08	0.06	0.05	0.04	0.02	0.24
<i>P. pictilis</i>									
USNM 874401	$\mu$	2.35	1.88	1.94	1.58	1.26	1.01	0.81	3.80
<i>n</i> = 15	s	0.20	0.13	0.15	0.10	0.08	0.07	0.03	0.19
<i>P. basiglans</i>									
USNM 874280	$\mu$	1.46	1.20	1.18	1.06	0.68	0.62	0.82	3.45
<i>n</i> = 15	s	0.13	0.05	0.08	0.07	0.04	0.04	0.04	0.24
<i>P. bifurcata</i>									
USNM 874306	$\mu$	1.50	1.16	1.14	1.01	0.68	0.62	0.78	3.67
<i>n</i> = 15	s	0.11	0.06	0.07	0.06	0.05	0.04	0.04	0.18
<i>P. pellita</i>									
USNM 883850	$\mu$	2.49	1.93	2.00	1.66	1.28	1.04	0.78	3.67
<i>n</i> = 15	s	0.17	0.09	0.13	0.08	0.07	0.06	0.04	0.23
<i>P. leporina</i>									
USNM 874336	$\mu$	3.61	2.57	2.70	2.26	1.65	1.38	0.71	4.07
<i>n</i> = 14	s	0.27	0.18	0.16	0.18	0.10	0.08	0.04	0.45
<i>P. humboldtensis</i>									
USNM 874722	$\mu$	2.23	1.87	1.88	1.55	1.18	0.99	0.84	3.53
<i>n</i> = 15	s	0.10	0.09	0.07	0.06	0.05	0.06	0.03	0.16
USNM 874719	$\mu$	2.72	2.10	2.19	1.79	1.33	1.17	0.77	3.78
<i>n</i> = 15	s	0.15	0.09	0.11	0.07	0.06	0.06	0.03	0.16
USNM 874725	$\mu$	2.58	2.16	2.15	1.73	1.38	1.20	0.84	3.77
<i>n</i> = 15	s	0.12	0.14	0.12	0.10	0.08	0.08	0.04	0.16
<i>P. hamlinensis</i>									
USNM 883215	$\mu$	1.84	1.15	1.29	1.07	0.73	0.59	0.63	4.13
<i>n</i> = 15	s	0.11	0.05	0.06	0.05	0.03	0.04	0.03	0.21

Table 1  
Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
<i>P. peculiaris</i>									
*USNM 883933	$\mu$	2.19	1.74	1.83	1.48	1.13	0.97	0.80	3.55
<i>n</i> = 15	s	0.09	0.07	0.10	0.05	0.06	0.05	0.03	0.22
USNM 874683	$\mu$	2.13	1.43	1.61	1.30	0.95	0.80	0.67	4.17
<i>n</i> = 15	s	0.14	0.07	0.07	0.05	0.05	0.05	0.03	0.15
USNM 883222	$\mu$	1.84	1.52	1.62	1.26	1.03	0.90	0.83	3.33
<i>n</i> = 15	s	0.07	0.05	0.05	0.04	0.03	0.04	0.03	0.24
USNM 883227	$\mu$	2.33	1.75	1.93	1.51	1.16	1.01	0.75	3.93
<i>n</i> = 15	s	0.10	0.10	0.10	0.07	0.09	0.08	0.02	0.15
USNM 883622	$\mu$	2.77	2.02	2.19	1.72	1.26	1.16	0.73	4.21
<i>n</i> = 15	s	0.11	0.07	0.07	0.06	0.05	0.04	0.02	0.16
USNM 883603	$\mu$	2.52	1.90	2.03	1.60	1.22	1.08	0.76	3.98
<i>n</i> = 15	s	0.15	0.09	0.10	0.06	0.08	0.05	0.02	0.18
<i>P. anguina</i>									
*USNM 874678	$\mu$	2.20	1.95	1.93	1.60	1.31	1.08	0.89	3.02
<i>n</i> = 15	s	0.13	0.13	0.14	0.08	0.12	0.07	0.03	0.68
USNM 883205	$\mu$	2.77	2.12	2.22	1.79	1.39	1.14	0.77	4.15
<i>n</i> = 15	s	0.23	0.14	0.18	0.14	0.09	0.09	0.03	0.21
<i>P. saxatilis</i>									
USNM 883237	$\mu$	1.16	1.11	1.04	0.83	0.80	0.62	0.96	3.23
<i>n</i> = 15	s	0.10	0.08	0.09	0.07	0.05	0.05	0.04	0.20
<i>P. variegata</i>									
USNM 883627	$\mu$	2.45	1.69	1.95	1.49	1.14	0.92	0.69	3.96
<i>n</i> = 15	s	0.12	0.07	0.09	0.08	0.05	0.04	0.03	0.13
USNM 883888	$\mu$	2.69	1.86	2.08	1.60	1.26	1.02	0.69	4.10
<i>n</i> = 15	s	0.12	0.10	0.11	0.09	0.08	0.08	0.03	0.16
USNM 874713	$\mu$	2.76	1.98	2.21	1.66	1.36	1.10	0.72	4.05
<i>n</i> = 15	s	0.10	0.07	0.08	0.05	0.05	0.06	0.02	0.17
USNM 883599	$\mu$	3.11	2.11	2.44	1.78	1.44	1.18	0.68	4.30
<i>n</i> = 15	s	0.15	0.13	0.12	0.08	0.08	0.09	0.04	0.19
USNM 883614	$\mu$	2.98	2.16	2.38	1.80	1.45	1.24	0.73	3.95
<i>n</i> = 15	s	0.14	0.10	0.13	0.09	0.11	0.08	0.03	0.19
*USNM 883624	$\mu$	2.46	1.79	1.98	1.53	1.21	1.02	0.73	3.85
<i>n</i> = 15	s	0.17	0.13	0.15	0.10	0.11	0.09	0.02	0.16
USNM 883583	$\mu$	2.31	1.70	1.82	1.41	1.14	0.96	0.73	3.95
<i>n</i> = 15	s	0.13	0.10	0.10	0.07	0.05	0.06	0.03	0.10
USNM 874721	$\mu$	2.34	1.73	1.86	1.48	1.15	0.96	0.74	3.85
<i>n</i> = 15	s	0.12	0.09	0.08	0.07	0.05	0.04	0.02	0.13
<i>P. hovinghi</i>									
USNM 874075	$\mu$	2.43	1.85	1.95	1.58	1.19	1.01	0.76	3.88
<i>n</i> = 15	s	0.13	0.07	0.08	0.06	0.04	0.07	0.03	0.21
<i>P. millenaria</i>									
USNM 874720	$\mu$	2.70	1.98	2.15	1.70	1.38	1.10	0.73	3.92
<i>n</i> = 15	s	0.16	0.13	0.12	0.06	0.10	0.08	0.03	0.18
<i>P. lentiglans</i>									
USNM 874724	$\mu$	1.63	1.09	1.15	0.99	0.71	0.56	0.67	4.05
<i>n</i> = 15	s	0.10	0.07	0.08	0.05	0.04	0.05	0.03	0.14
USNM 854540	$\mu$	1.49	0.92	1.04	0.86	0.57	0.45	0.62	3.93
<i>n</i> = 15	s	0.05	0.02	0.03	0.02	0.02	0.02	0.02	0.11
<i>P. plicata</i>									
USNM 883594	$\mu$	2.59	1.99	2.18	1.63	1.34	1.11	0.77	3.90
<i>n</i> = 15	s	0.17	0.12	0.16	0.08	0.10	0.07	0.03	0.16



Table 1  
Continued.

		SH	SW	HBW	WBW	AH	AW	SS	WH
<i>P. fusca</i>									
USNM 883439	μ	2.86	1.99	2.18	1.74	1.33	1.08	0.70	4.05
<i>n</i> = 15	s	0.18	0.11	0.13	0.09	0.12	0.06	0.03	0.19
USNM 883573	μ	3.50	2.37	2.64	2.06	1.56	1.29	0.68	4.33
<i>n</i> = 13	s	0.37	0.20	0.28	0.18	0.15	0.12	0.04	0.26
<i>P. chamberlini</i>									
USNM 854786	μ	2.83	1.96	2.16	1.74	1.24	1.16	0.69	4.33
<i>n</i> = 15	s	0.18	0.13	0.14	0.10	0.09	0.09	0.04	0.18
USNM 854784	μ	4.05	2.88	3.13	2.43	1.91	1.54	0.71	4.82
<i>n</i> = 15	s	0.31	0.15	0.24	0.13	0.14	0.13	0.03	0.20
<i>P. inopinata</i>									
USNM 854783	μ	3.27	1.98	2.26	1.79	1.25	1.03	0.61	4.75
<i>n</i> = 15	s	0.12	0.07	0.09	0.09	0.05	0.06	0.03	0.16
USNM 854785	μ	2.45	1.52	1.74	1.41	0.95	0.79	0.62	4.29
<i>n</i> = 13	s	0.12	0.09	0.10	0.08	0.05	0.06	0.02	0.14
<i>P. nonaria</i>									
USNM 883566	μ	2.66	1.71	1.98	1.55	1.17	0.90	0.65	4.13
<i>n</i> = 15	s	0.11	0.09	0.06	0.05	0.06	0.07	0.03	0.16
<i>P. transversa</i>									
USNM 883221	μ	2.15	1.50	1.68	1.28	1.27	0.95	0.69	3.93
<i>n</i> = 15	s	0.15	0.12	0.09	0.09	0.10	0.09	0.03	0.15
USNM 883422	μ	2.79	1.81	2.11	1.57	1.27	0.98	0.65	4.40
<i>n</i> = 15	s	0.12	0.07	0.11	0.05	0.05	0.05	0.02	0.18
USNM 883210	μ	2.71	1.91	2.14	1.66	1.26	1.08	0.71	4.15
<i>n</i> = 15	s	0.11	0.11	0.09	0.06	0.06	0.05	0.04	0.18
USNM 883481	μ	2.49	1.71	1.99	1.47	1.27	0.95	0.69	3.93
<i>n</i> = 15	s	0.21	0.12	0.16	0.09	0.10	0.09	0.03	0.15
USNM 883597	μ	2.99	2.10	2.33	1.76	1.41	1.16	0.70	4.32
<i>n</i> = 15	s	0.12	0.07	0.11	0.06	0.08	0.08	0.02	0.20
USNM 883572	μ	2.70	1.87	2.07	1.66	1.25	1.01	0.69	3.97
<i>n</i> = 15	s	0.19	0.11	0.11	0.09	0.08	0.06	0.03	0.19

rial was collected during the course of the field survey by washing stones or sweeping soft sediment or aquatic vegetation with a small hand sieve. Samples were placed in glass jars, narcotized with crushed menthol crystals for about 13 hours, fixed in dilute (4%) formalin, and then preserved in 70% ethanol. Legal coordinates and land ownership status were noted for each site (from 1:100,000 topographic maps), as were elevation and a variety of habitat data. Distribution maps were prepared from spatial databases obtained from the United States Geological Survey digital line graph (for drainage and political boundaries). Locations of snail-positive sites were digitized from the 1:100,000 maps. Mapping data were processed in Arc/Info with dBase5.0.

Institutional repositories of examined specimens are indicated by the following abbreviations: FMNH, Field Museum of Natural History, Chicago; SBMNH, Santa Barbara Museum of Natural History; UCM, University of Colorado Museum, Boulder; UMMZ, University of Michigan Museum of Zoology, Ann Arbor; USNM, for-

mer United States National Museum, collections now in National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Shell parameters were obtained from one or more randomly selected samples of about 15 adult specimens (as indicated by completion of the inner shell lip) for each new species using methods of Hershler (1989). Descriptive statistics for these parameters were generated using SYSTAT (Wilkinson, 1986) and are summarized in Table 1. Shells, opercula, and radulae were cleansed in commercial bleach (CLOROX), rinsed in distilled water, mounted on stubs, and then studied and photographed using a Leica 440 Scanning Electron Microscope (SEM).

Body pigmentation was studied for alcohol-preserved material and, although most of this material was recently collected, color has probably faded in older lots. Anatomical study was of specimens soaked in Bouin's Solution to remove inorganic shell material. Animals were dissected in dilute Bouin's Solution using methods of Hershler (1994:2). Crude sections of female capsule gland

and male prostate gland were cut using iridectomy scissors. Anatomical illustrations were prepared from camera lucida drawings. Five or six specimens of each sex (paratypes or topotypes) were usually dissected for each species, although additional series were added for species that are either widely distributed or show significant geographic variation in shell features. For description of penial variation, a series of 10–30 penes was excised and studied from all available samples for each species. Terminology of penial morphology and glands is that of Hershler (1994:5–6; also see Figure 26).

The following morphologic features were scrutinized when preparing species descriptions:

*Shell*: shape, height, width, number of whorls, number of protoconch whorls, protoconch diameter, protoconch sculpture, shape of teleoconch whorls, aperture shape, relationship between inner lip and body whorl, thickness of lip, width of columellar shelf, shape and inclination of outer lip, umbilicus development, periostracum color.

*Operculum*: shape, color, number of whorls, location of nucleus, frilling of whorl outlines on dorsal surface, development of rim along outer margin, thickening of attachment scar margin.

*Digestive system*: length and width of radular ribbon, number of tooth rows; width, dorsal indentation, number of lateral cusps, shape of central cusp, size of basal cusps, shape of basal tongue, depth of basal sockets on central radular teeth; tooth formula, flexure of neck, length of outer wing relative to cutting edge of lateral radular teeth; number of cusps, length of cutting edge relative to overall length of inner and outer marginal teeth; length of stomach relative to style sac, relative sizes of anterior and posterior stomach chambers, size of stomach caecum.

*Body pigmentation*: color, intensity, location of pigmentation on cephalic tentacles, snout, foot, opercular lobe, neck, pallial roof, visceral coil, penis.

*Pallial cavity*: number of ctenidial filaments, presence of pleats on filaments, posterior extent of ctenidium; osphradium size, shape and position relative to ctenidial axis; orientation of renal gland, thickening of kidney opening, extent to which rectum overlaps genital ducts.

*Female animal*: number of whorls occupied by ovary, length of ovary relative to digestive gland behind stomach, anterior extension of ovary, extent of pallial portion of albumen gland relative to overall length of gland, relative lengths of albumen and capsule glands, shape of capsule gland in section, development of rectal furrow on capsule gland, extent to which ventral channel overlaps capsule gland, development of longitudinal fold of ventral channel; shape, position, and anterior extension of genital aperture; shape and number of oviduct coils, position of junction of oviduct and bursal duct, length and width of bursa copulatrix relative to albumen gland; shape, orientation relative to albumen gland, posterior extent of bursa copulatrix; origin, length and width (relative to bursa copulatrix) of bursal duct; position of bursal duct relative to

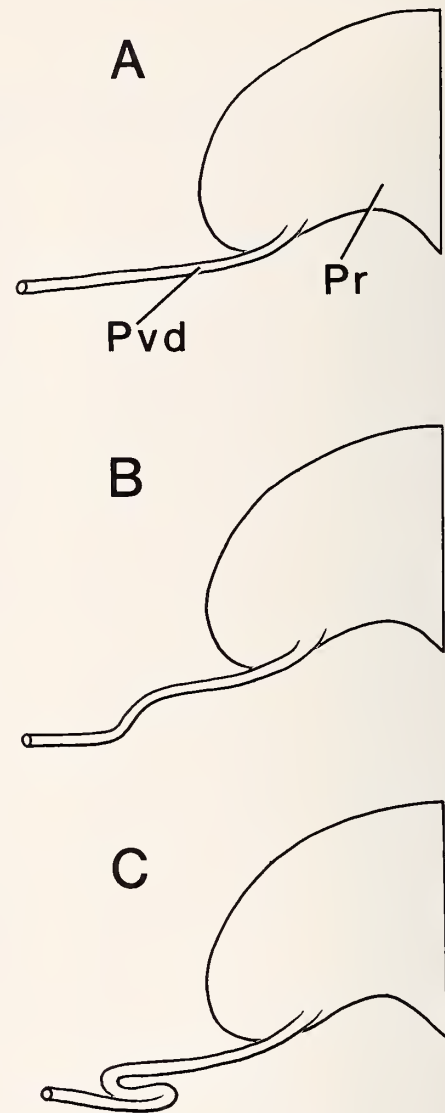


Figure 2

Schematic diagram of the anterior portion of the prostate gland (viewed from the left side) showing variation in coiling of the pallial vas deferens. A. Vas deferens straight. B. With weak undulation. C. With prominent, reflexed bend. Pr = prostate gland, Pvd = pallial vas deferens.

surface of albumen gland; size (relative to length of bursa copulatrix), shape, position of seminal receptacle.

*Male animal*: number of whorls occupied by testis, length of testis relative to digestive gland behind stomach, anterior extension of testis; size, shape of prostate gland, extent of pallial portion of prostate gland, shape of prostate gland in section; shape of proximal portion of pallial vas deferens (Figure 2); size of penis relative to head; shape and folding of base of penis; length (relative to base), width, shape, orientation of filament and lobe;

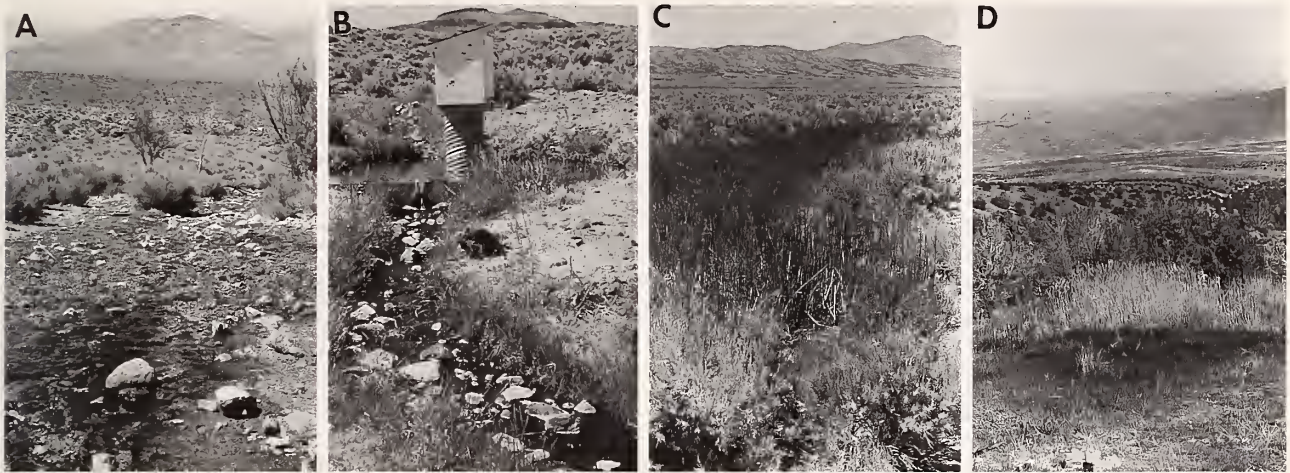


Figure 3

Representative Great Basin springs. A. Horseshutem Springs, nestled along the western flank of the Spring Mountains (1480 m elevation) in southeast Nevada. This small rheocene, severely impacted by cattle, is the type locality of *P. turbatrix*. Photograph by D. Sada, July, 1995. B. One of many small, thermal rheocrenes in the Mud Meadow drainage in northwest Nevada. Water temperature at this site was 39°C. and *P. notidicola* was found living in a moistened zone just outside the water. Note the artificial impoundment and old gauge box at the source of this spring. Photograph by G. Vinyard, August, 1991. C. Unnamed spring in Park Valley, northwest Utah. One of many highly mineralized springs in the Bonneville Basin inhabited by *P. kolobensis*. Photograph, August, 1993. D. Unnamed springs in the Simpson Mountains (1779 m elevation), overlooking the Old River Bed in southern Utah. These small, mineralized (1126 micromhos/cm) rheocrenes compose the type locality of *P. transversa*. Photograph, May, 1993.

number, size, position, orientation, apparent fusion of glands on penis; shape, position of penial duct.

Previously described species are treated only when new records were obtained from the field survey. Literature compilations pertaining to these snails are in Taylor (1975) and my recent review of *Pyrgulopsis* (Hershler, 1994). Synonomies for these taxa are not intended to be complete, but instead detail original citation of species (and synonyms), assignment to *Pyrgulopsis*, treatments of material from the study area, and pertinent references to the broader works listed above. A common name is proposed for each new species to facilitate their reference by governmental agencies.

### NATURAL HISTORY

*Pyrgulopsis* are widespread within the Great Basin where they occur in a variety of relatively small, usually fishless, spring-fed water bodies (Figures 3–5). These animals also historically occurred in a few of the Great Basin lakes, with the main example provided by *P. nevadensis* (Stearns, 1883), which lived in Pyramid Lake (of the Lahontan Basin) until becoming extinct around the turn of the century. Members of this genus have not been found in any of the rivers of the Great Basin. The most common habitat for these snails is a rheocene, or a spring which emerges from the ground as a flowing stream. *Pyrgulopsis* also occur in limnocrenes, in which the headspring forms a natural pool (which is drained by a flowing

stream), and helocrenes, springs that comprise marshlike situations. Waters harboring *Pyrgulopsis* range from small seeps with miniscule discharge and depth of 1 cm or less, to large springs such as those feeding Clear Lake in southern Utah, whose discharge is about 6.8 m<sup>3</sup>/sec (Mundorff, 1971:62). While most of these springs are of medium temperature (e.g., 10–21°C.), snails were also found in more than 50 thermal springs (e.g., those having temperature greater than 21°C.; per Garside & Schilling, 1979:1). While most of these springs were in the 22–35° range, it is worth noting that in the two cases in which even warmer (ca. 39°C.) water was involved (i.e., springs in Mud Meadows harboring *P. notidicola*; described below), most of the snails seen were madicolous, inhabiting a moistened zone around the margins of the spring. While most of the springs were of low to medium conductivity (e.g., 200–600 micromhos/cm), *Pyrgulopsis* were collected from more than 50 brackish springs (having greater than 1 gm/l total dissolved solids; Todd, 1980), most of which were along the margins of the Great Salt Lake Desert (and harbored *P. kolobensis*).

*Pyrgulopsis* often decline dramatically in density downflow from spring sources, presumably reflecting their requirement for the well-known stable temperature, chemistry, and flow regime characterizing headsprings (Deacon & Minckley, 1974). This pattern of distribution is most pronounced in smaller springs, while in larger habitats *Pyrgulopsis* may occur far downstream from spring sources.

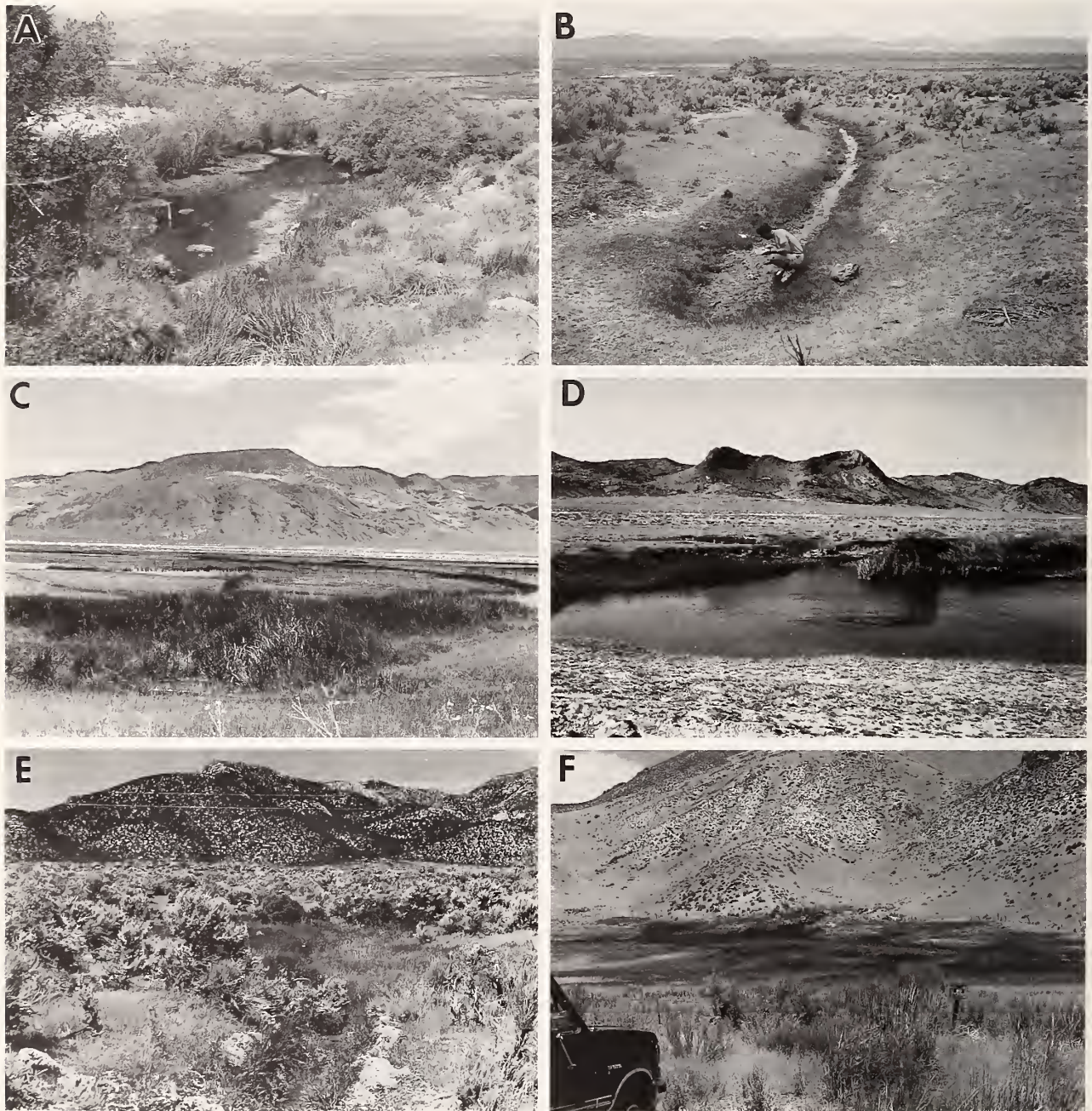


Figure 4

Representative Great Basin springs. A. The northernmost spring in the Flag Spring complex, White River Valley, Nevada. This limnocene (pool diameter about 15 m) is the type locality of *P. sathos*, which was collected along the margins of the 14 m diameter pool. *Pyrgulopsis breviloba* was abundant in the outflow channel below the pool. Photograph, June 1992. B. The southernmost spring in the Emigrant Springs complex, White River Valley, Nevada. *Pyrgulopsis gracilis* and *P. marcida* co-occur in this small rheocene, which is highly impacted by cattle. Photograph, June 1992. C. Unnamed basin floor spring in Fish Lake Valley, Nevada. The source of this spring is a small (2 m diameter), thermal (26°C.) limnocene. The narrow outflow is the type locality of *P. ruinosa*, now believed to be extinct. Photograph, July 1988. D. Big Warm Spring, a large, thermal (30.5°C.) limnocene in Duckwater Valley, Nevada. This is the type locality of *P. papillata*, and *P. villacampae* also is present. Photograph, D. Sada, October 1992. E. One of many small rheocrenes that compose a large wetland along the southeastern edge of Steptoe Valley near Ely, Nevada, which contains a series of locally endemic snail species (as well as *P. kolobensis*). This site is the type locality of *P. sulcata*. Photograph, August 1991. F. Series of small rheocrenes along Pine Creek, Humboldt River drainage, Nevada, which harbor *P. gibba*. Photograph, July 1991.



Figure 5

Representative Great Basin springs. A. Wetland fed by a series of small, mineralized (ca. 1000 micromhos/cm) springs, perched in the Shoshone Range above Reese River Valley, Nevada. This is the type locality of *P. sadai*, which was found in only one of these springs (in a small area of about 1 m<sup>2</sup>), all of which were highly degraded by cattle. Photograph, July 1994. B. Bar M Spring, one of the many brackish springs along the northern edge of the Great Salt Lake (Utah) that harbors *P. kolobensis*. Photograph, July 1993. C. Salt Spring, another brackish spring in northern Utah harboring *P. kolobensis*. Photograph, May 1993. D. Unnamed springs along the eastern flank of the White Rock Mountains (2180 m elevation), overlooking Hamlin Valley, Utah. This is the type locality of *P. hamlinensis*, which occurred abundantly in the dense stand of watercress lining the small stream. Photograph, May 1993. E. Broad (8 m), shallow, spring-fed stream tributary to Etna Reservoir, Grouse Creek Valley, Utah, harboring *P. variegata*. Photograph, July 1993. F. Series of small rheocrenes, Thousand Springs Creek drainage, Nevada, comprising the type locality of *P. millenaria*. Photograph, August 1992.

*Pyrgulopsis* are most commonly found among aquatic vegetation, especially Cress (*Rorippa*<sup>2</sup>), which often forms dense mats lining outflows of small springs. In larger limnocrenes (which often are thermal), snails may be found on other aquatic plants such as Bladderwort (*Utricularia*), or on the bases of riparian Spike rush (*Eleocharis*) or Tule (*Scirpus*). Snails are also often found on hard substrates such as bedrock or pieces of travertine. *Pyrgulopsis* are rarely found on or in soft sediment. Although quantitative sampling of snails was not pursued during this project, the densities of 1000–10,000 snails/m<sup>2</sup> reported for several limnocrene springs in eastern Nevada by Deacon et al. (1980) are probably typical for that habitat in the Great Basin, and considerably less than those of snails inhabiting the smaller rheocrenes. As an indication of the typical local abundance of these animals, a few minutes of sampling at a site usually yielded several hundred living individuals.

*Pyrgulopsis* are not only found in basin floor springs, which often line the perimeter of dry lake beds and whose outflows coalesce to form large marshes, but also in springs farther up the mountain slopes as well as in spring brooks and streams coursing along well-defined canyons. The snails were collected from sites ranging up to about 2440 m elevation, but appeared to “drop out” in higher alpine situations. For the most part, members of this fauna are distributed in an allopatric fashion. Sympatry of two (and rarely three) congeners was documented at only 14 of the more than 400 sites listed herein, most of which were springs in Duckwater and Steptoe Valley where series of locally endemic species occur. Although the fauna includes several widespread species, notably *P. gibba* and *P. kolobensis*, local endemism is a more common feature. Note that 22 of the 58 new species appear to be restricted to single localities. Details of biology have not been studied for *Pyrgulopsis* of the Great Basin. In the sole detailed study of biology of any species of the genus, Mladenka (1992) determined that *P. bruneauensis*, which is endemic to thermal springs in the Snake River drainage of southern Idaho, is a non-selective grazer of algae and diatoms. As with other congeners, the Great Basin species are oviparous, with females depositing single, small egg capsules on hard substrates.

Two of the species described herein (*P. carinata* and *P. ruinosa*) apparently have become extinct during the past one or two decades. Relatively few of the collecting sites are in pristine condition, with livestock grazing being the predominant source of disturbance. Smaller, basin floor springs in particular were often profoundly disturbed by cattle, which modify the habitat both physically and chemically by trampling, removing aquatic and riparian vegetation, and depositing urine and feces. The resulting habitat often is largely unsuitable for *Pyrgulopsis*, al-

though snails may persist in a small, upflow “refuge” of clean, flowing water which cows cannot reach. Additional, but less prevalent sources of disturbance are related to human residential and recreational activities, notably diversion and/or withdrawal of water. Exotic biota also may pose a serious threat to these populations, particularly crayfish, which have been widely introduced into the region’s waters (Bouchard, 1978; Johnson, 1986) and, although omnivorous, often feed on small gastropods (Covich, 1978; Vermeij & Covich, 1978). An Asiatic gastropod, *Melanoides tuberculata* (Müller, 1774), now thrives in many of the warm springs of the Great Basin and may be displacing native prosobranch snails here and elsewhere in the West (see Murray, 1970; Williams et al., 1985), although rigorous documentation of this phenomenon and elucidation of its mechanism are lacking.

## SYSTEMATICS

### Family HYDROBIIDAE Troschel, 1857

#### *Pyrgulopsis* Call & Pilsbry, 1886

**Type species:** *Pyrgula nevadensis* Stearns, 1883; original designation.

**Diagnosis:** A North American freshwater genus distinguished from other taxa assigned to the subfamily Nymphophilinae by the combination of small size, relatively thin, and generally ovate to ovate-conic shell, and penis having relatively few glands. Differs from similar *Nymphophilus* Taylor, 1966b (locally endemic in northern Mexico) in several features of the radular teeth (e.g., narrower central teeth, narrower basal tongue on the central teeth, narrower central cusps on the central and lateral teeth), simpler gonadal morphology, longitudinal (not transverse) bursa copulatrix, and superficial (not raised) position of the vas deferens on the neck.

**Remarks:** Phylogenetic relationships among the new taxa described herein are not known. Thus, for sake of convenience and to aid the reader attempting to identify material, these species instead are treated according to their geographic distributions, which are grouped into major hydrographic units as indicated below. Note that although local endemism is frequent in this fauna, several species occur in more than one of these drainages.

(a) Death Valley system. The hydrobiid fauna of this large drainage, which may or may not have emptied into the Colorado River during the Quaternary (Brown & Rosen, 1995), was recently reviewed by Hershler & Pratt (1990). During the current survey, new material was obtained from a few portions of the drainage in southwestern Nevada.

(b) Colorado River basin. This includes the current Colorado River drainage in southern Nevada as well as several large basins in the eastern half of the state that drained to the Colorado in pluvial times (Hubbs & Miller, 1948).

<sup>2</sup> Note that the widespread Watercress is often segregated as *Nasturtium* (Nelson, 1992).

(c) Isolated basins in Nevada. This includes a large number of valleys whose pluvial waters were not integrated with either Lake Lahontan or Lake Bonneville.

(d) Lahontan Basin. A very large pluvial drainage encompassing the Carson, Humboldt, Susan, Quinn, Truckee, and Walker River basins.

(e) Oregon Lakes. An area of isolated basins in southeast Oregon and northeast California, north of the Lahontan Basin.

(f) Bonneville Basin. A huge drainage, occupying much of western Utah, and portions of southeast Idaho and eastern Nevada, which contained the largest pluvial lake in the Great Basin.

Scanning electron micrographs of shells of each new species are shown in Figures 6–10. Scanning electron micrographs of shell protoconch (Figure 11), operculum (Figures 12, 13), and radula (Figures 14–16) are illustrated for small subsets of the new species in order to show variation in relevant features. Type and nontype shells (Figures 17–25), and distal female genitalia and penis (Figures 26–48) are illustrated for each of the new species following the text, along with maps showing distribution of the species (Figures 49–56).

## SYSTEMATICS

### Species from the Death Valley System

#### *Pyrgulopsis micrococcus* (Pilsbry, 1893)

- Ammicola micrococcus* Pilsbry in Stearns, 1893:277, fig. 1.  
*Fontelicella (Microammicola) micrococcus* (Pilsbry in Stearns, 1893), Gregg & Taylor, 1965:109 [transfer to *Fontelicella (Microammicola)*].  
*Fontelicella micrococcus* (Pilsbry in Stearns, 1893), Taylor, 1975:123 [literature compilation].  
*Pyrgulopsis micrococcus* (Pilsbry in Stearns, 1893), Hershler & Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Hershler, 1994:50, 52 [figures, literature compilation].

**Diagnosis:** Small to medium-sized, with sub-globose to ovate-conic shell. Penis medium-sized, filament medium length, lobe short. Penial ornament a small-medium terminal gland.

**Type locality:** Small spring in Oasis Valley, Nevada.

**Remarks:** *Pyrgulopsis micrococcus* is contrasted with *P. turbatrix* below. This species is widespread in the eastern portion of the Death Valley system (Hershler & Pratt, 1990:fig. 5). Collections made during the survey are all in the immediate vicinity of the type locality. Note that populations from Frenchman Flat (Cane Spring) and northern end of the Spring Mountains (Cold Creek, Willow Creek) in southern Nevada assigned to this species by Hershler & Pratt (1990) are herein transferred to *P. turbatrix* (described below). The distribution of this species is shown in Figure 49.

**Material examined:** NEVADA. *Nye County*: Spring, ad-

acent to HWY 95, Oasis Valley, Amargosa River drainage, T. 10 S, R. 47 E, SE ¼ section 32, USNM 874778.—Spring, east of HWY 95, east end of Oleo Road, Oasis Valley, Amargosa River drainage, T. 11 S, R. 47 E, NW ¼ section 10, USNM 874771.—Spring, 2 km northwest of Beatty, Oasis Valley, Amargosa River drainage, T. 12 S, R. 47 E, SW ¼ section 5, USNM 874758.

### Species from the Colorado River Drainage

#### *Pyrgulopsis fausta* Hershler, sp. nov.

##### Corn Creek pyrg

(Figures 6A, 12A, 17A, 26A–C)

**Etymology:** From *faustus* (Latin), lucky; referring to the good fortune that this locally endemic species persists despite a long and continuing period of extensive development in the vicinity of Las Vegas, Nevada.

**Diagnosis:** Small, with sub-globose shell. Penis large, filament medium length, lobe short. Penial ornament a small terminal gland, large penial gland, small Dg1, dot-like Dg2, large Dg3, and large ventral gland.

**Description:** Shell (Figures 6A, 17A) sub-globose, width/height, 83–94%; height 1.4–1.7 mm; width, 1.3–1.5 mm; whorls, 3.25–3.75. Protoconch 1.3 whorls, diameter 0.33 mm, initial 1.0 whorl finely wrinkled (sculpture coarser at apex), later portion near smooth, sculpture occasionally coalescing to form weak spiral elements. Teleoconch whorls moderately convex, usually shouldered. Aperture broadly ovate, adnate or slightly separated from body whorl. Inner lip slightly thickened, without columellar shelf. Outer lip slightly thickened, weakly prosocline, without sinuation. Umbilicus rimate or perforate. Periostracum light tan.

Operculum (Figure 12A) ovate, amber; nucleus slightly eccentric; dorsal surface weakly frilled; outer margin sometimes having weak rim. Attachment scar sometimes slightly thickened between nucleus and inner edge.

Radula 600 × 80 μm, with 75 rows of teeth. Central tooth 21 μm wide, with medium indented dorsal edge; lateral cusps 5–6; central cusp narrow, daggerlike; basal cusps small. Basal tongue narrow V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)–1–5; weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 25–28 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 34–37 cusps; cutting edge occupying 20% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles unpigmented or having a few scattered brown granules on dorsal surfaces. Snout, foot unpigmented; opercular lobe unpigmented or having band of grey-black subepithelial pigment along inner edge. Neck having scattered grey, subepithelial pigment. Pallial roof,

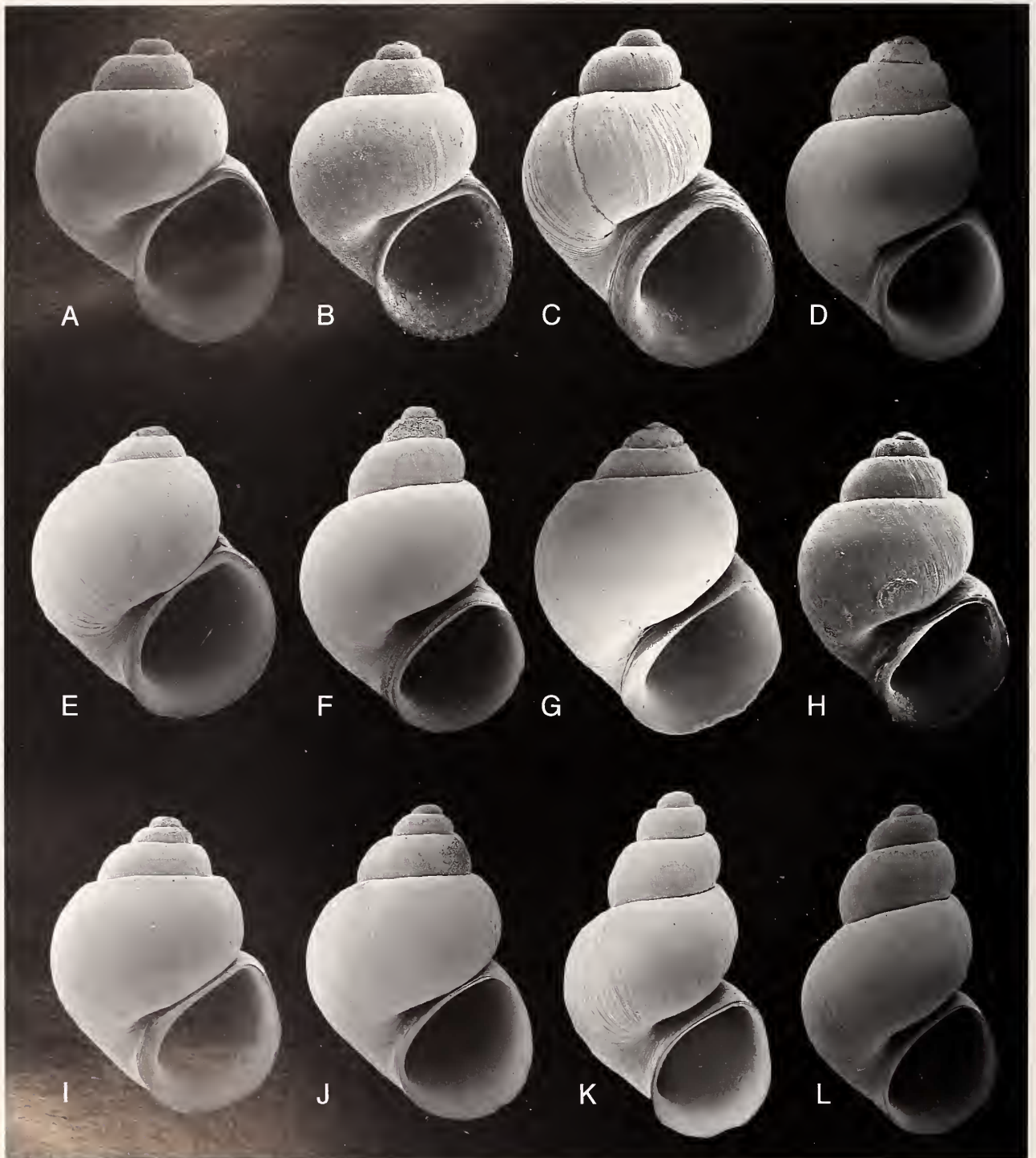


Figure 6

Shells of *Pyrgulopsis* species. A. *P. fausta*, USNM 860765 (shell height, 1.7 mm). B. *P. deaconi*, USNM 860676 (1.9 mm). C. *P. coloradensis*, USNM 860677 (1.6 mm). D. *P. montana*, USNM 860694 (2.5 mm). E. *P. hubbsi*, USNM 860690 (3.1 mm). F. *P. sathos*, USNM 860691 (3.0 mm). G. *P. breviloba*, USNM 860689 (1.8 mm). H. *P. lata*, USNM 860697 (1.9 mm). I. *P. gracilis*, USNM 860698 (1.8 mm). J. *P. marcida*, USNM 860711 (3.0 mm). K. *P. turbatrix*, USNM 860699 (3.0 mm). L. *P. sterilis*, USNM 860714 (3.6 mm).



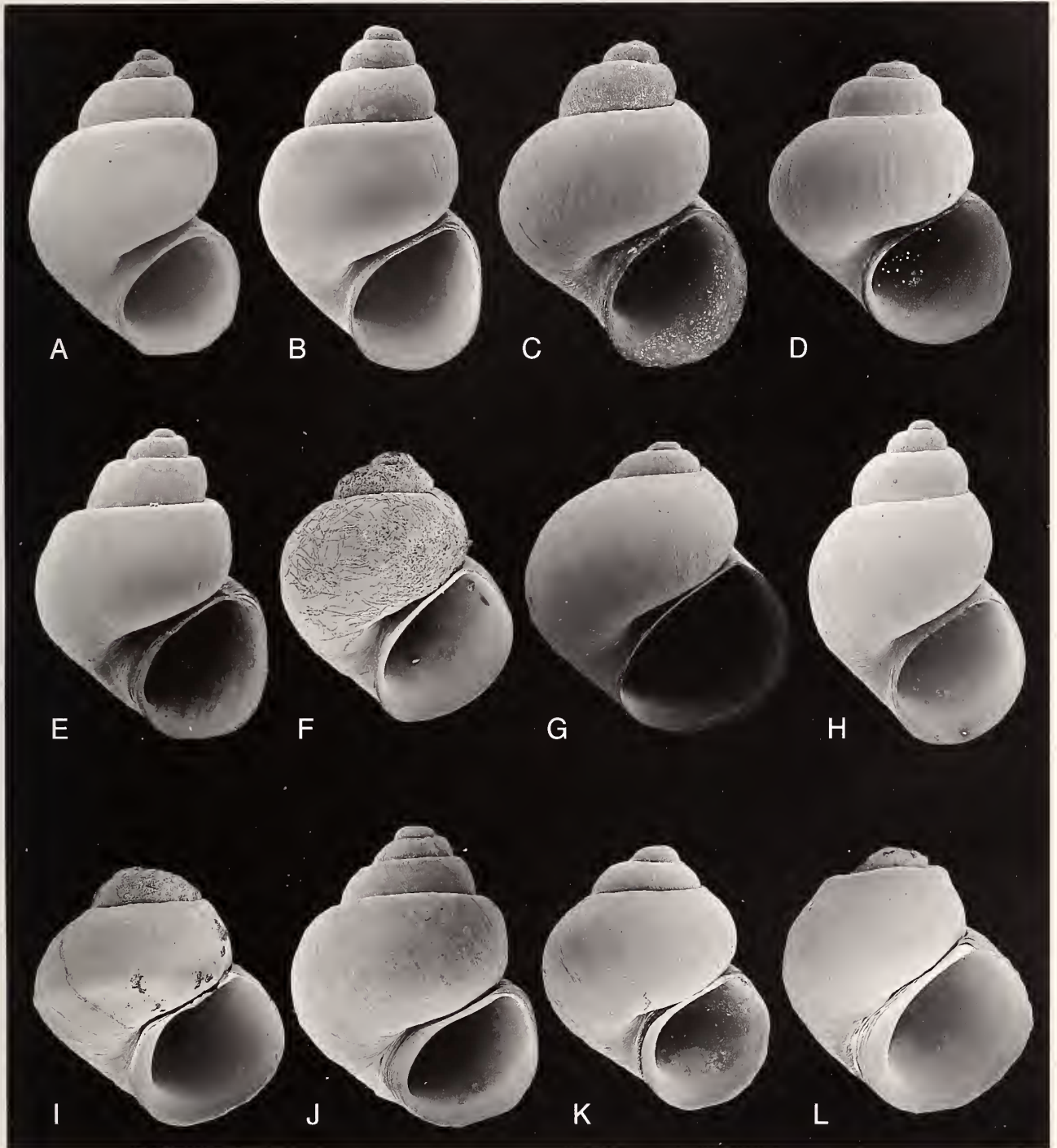


Figure 7

Shells of *Pyrgulopsis* species. A. *P. ruinosa*, USNM 860700 (2.8 mm). B. *P. sublata*, USNM 860724 (2.4 mm). C. *P. lockensis*, USNM 860679 (1.9 mm). D. *P. papillata*, USNM 860678 (1.9 mm). E. *P. carinata*, USNM 860680 (2.1 mm). F. *P. aloba*, USNM 860681 (1.2 mm). G. *P. villacampae*, USNM 860712 (2.4 mm). H. *P. anatina*, USNM 860710 (2.3 mm). I. *P. planulata*, USNM 860686 (1.3 mm). J. *P. sulcata*, USNM 860683 (1.4 mm). K. *P. orbiculata*, USNM 860682 (2.1 mm). L. *P. neritella*, USNM 860684 (1.3 mm).

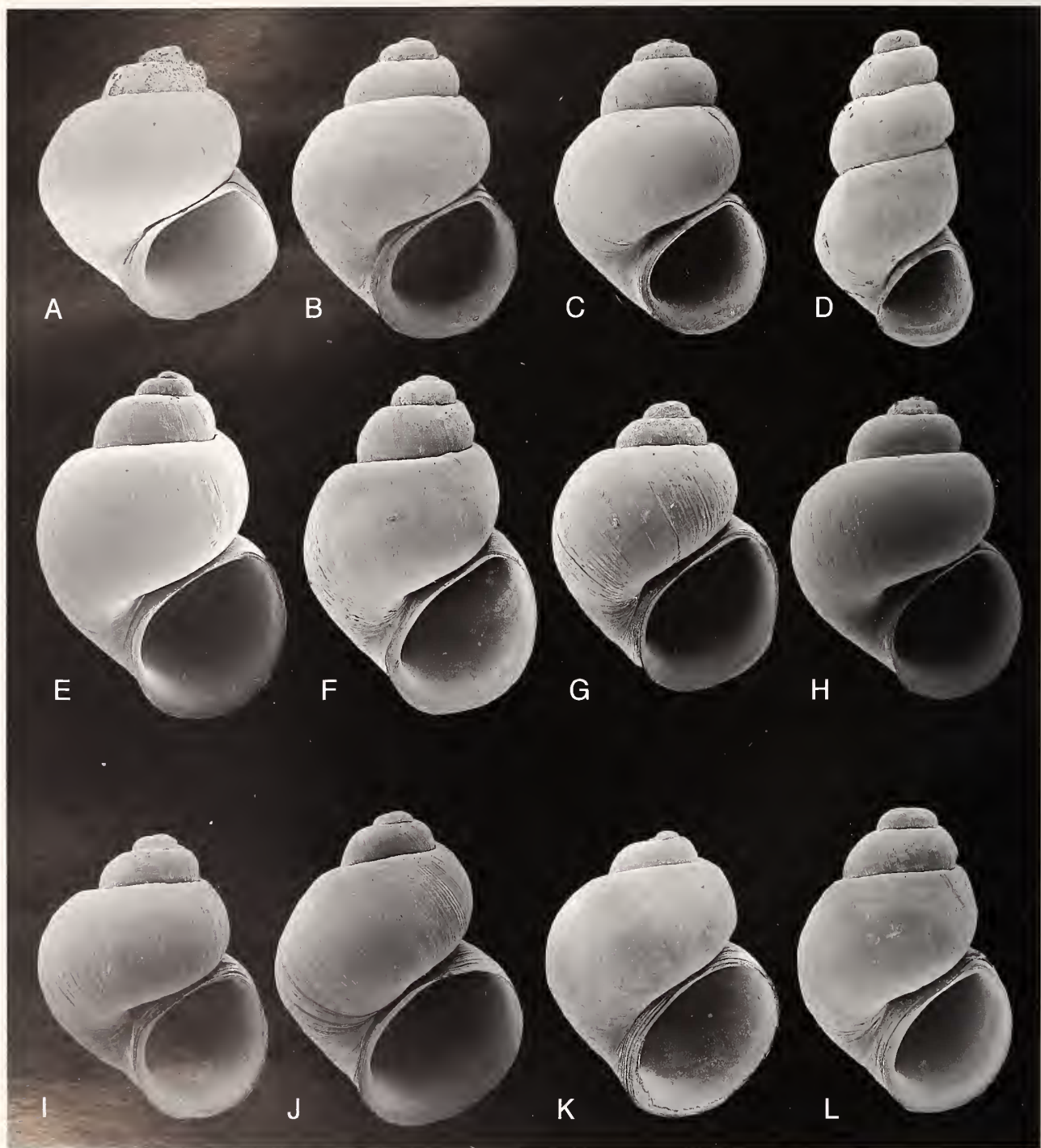


Figure 8

Shells of *Pyrgulopsis* species. A. *P. landyei*, USNM 860685 (1.3 mm). B. *P. serrata*, USNM 860719 (3.2 mm). C. *P. cruciglans*, USNM 860719 (3.3 mm). D. *P. dixensis*, USNM 860688 (1.6 mm). E. *P. aurata*, USNM 860696 (2.5 mm). F. *P. longiglans*, USNM 860701 (3.4 mm). G. *P. militaris*, USNM 860704 (2.4 mm). H. *P. unbilicata*, USNM 860705 (3.2 mm). I. *P. linaria*, USNM 860706 (2.6 mm). J. *P. notidicola*, USNM 860707 (3.0 mm). K. *P. vinyardi*, USNM 860708 (2.6 mm). L. *P. imperialis*, USNM 860716 (2.3 mm).

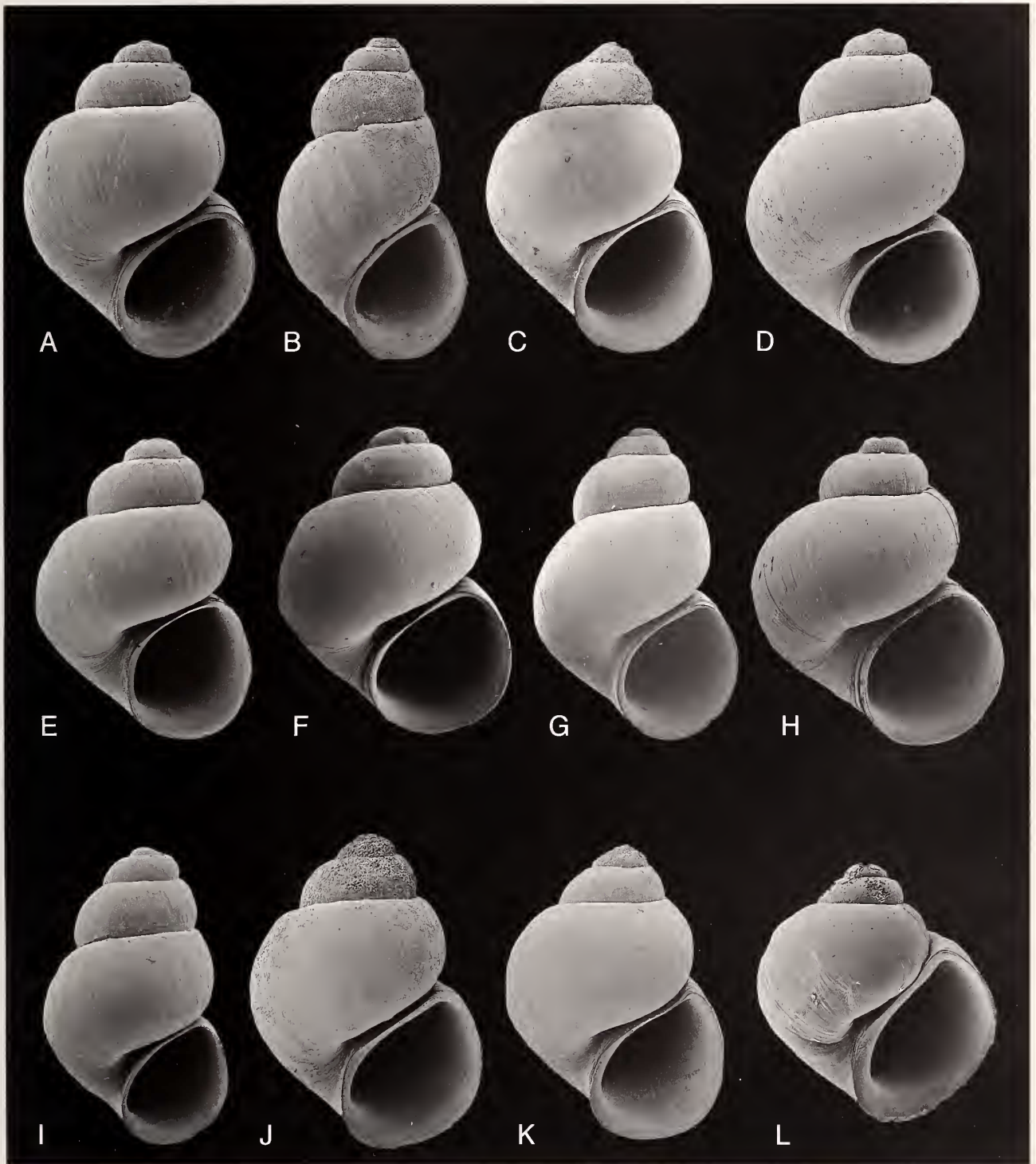


Figure 9

Shells of *Pyrgulopsis* species. A. *P. sadai*, USNM 860702 (3.8 mm). B. *P. augustae*, USNM 860687 (3.3 mm). C. *P. pictilis*, USNM 860713 (2.6 mm). D. *P. basiglans*, USNM 860692 (2.8 mm). E. *P. bifurcata*, USNM 860693 (2.3 mm). F. *P. pellita*, USNM 860715 (2.5 mm). G. *P. leporina*, USNM 860717 (3.6 mm). H. *P. humboldtensis*, USNM 860718 (2.2 mm). I. *P. hamlinensis*, USNM 860695 (1.9 mm). J. *P. peculiaris*, USNM 860703 (2.0 mm). K. *P. anguina*, USNM 860725 (2.5 mm). L. *P. saxatilis*, USNM 860726 (1.2 mm).

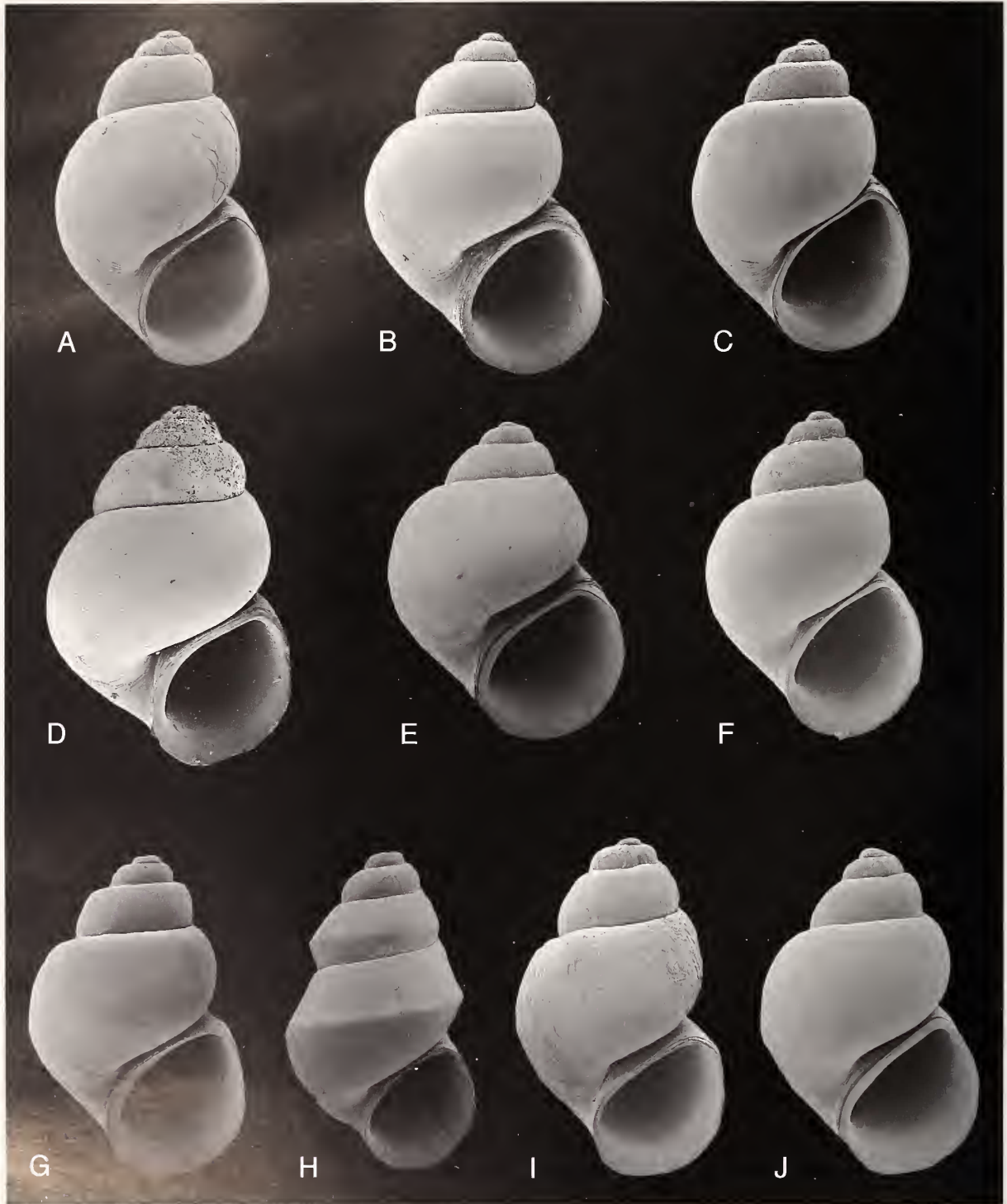


Figure 10

Shells of *Pyrgulopsis* species. A. *P. variegata*, USNM 860723 (2.3 mm). B. *P. hovinghi*, USNM 860720 (2.6 mm). C. *P. millenaria*, USNM 860721 (2.4 mm). D. *P. lentiglaus*, USNM 860722 (1.7 mm). E. *P. plicata*, USNM 860727 (2.2 mm). F. *P. fusca*, USNM 860728 (2.7 mm). G. *P. chamberlini*, USNM 860729 (2.3 mm). H. *P. inopinata*, USNM 860730 (2.7 mm). I. *P. nonaria*, USNM 860731 (2.6 mm). J. *P. transversa*, USNM 860732 (2.3 mm).

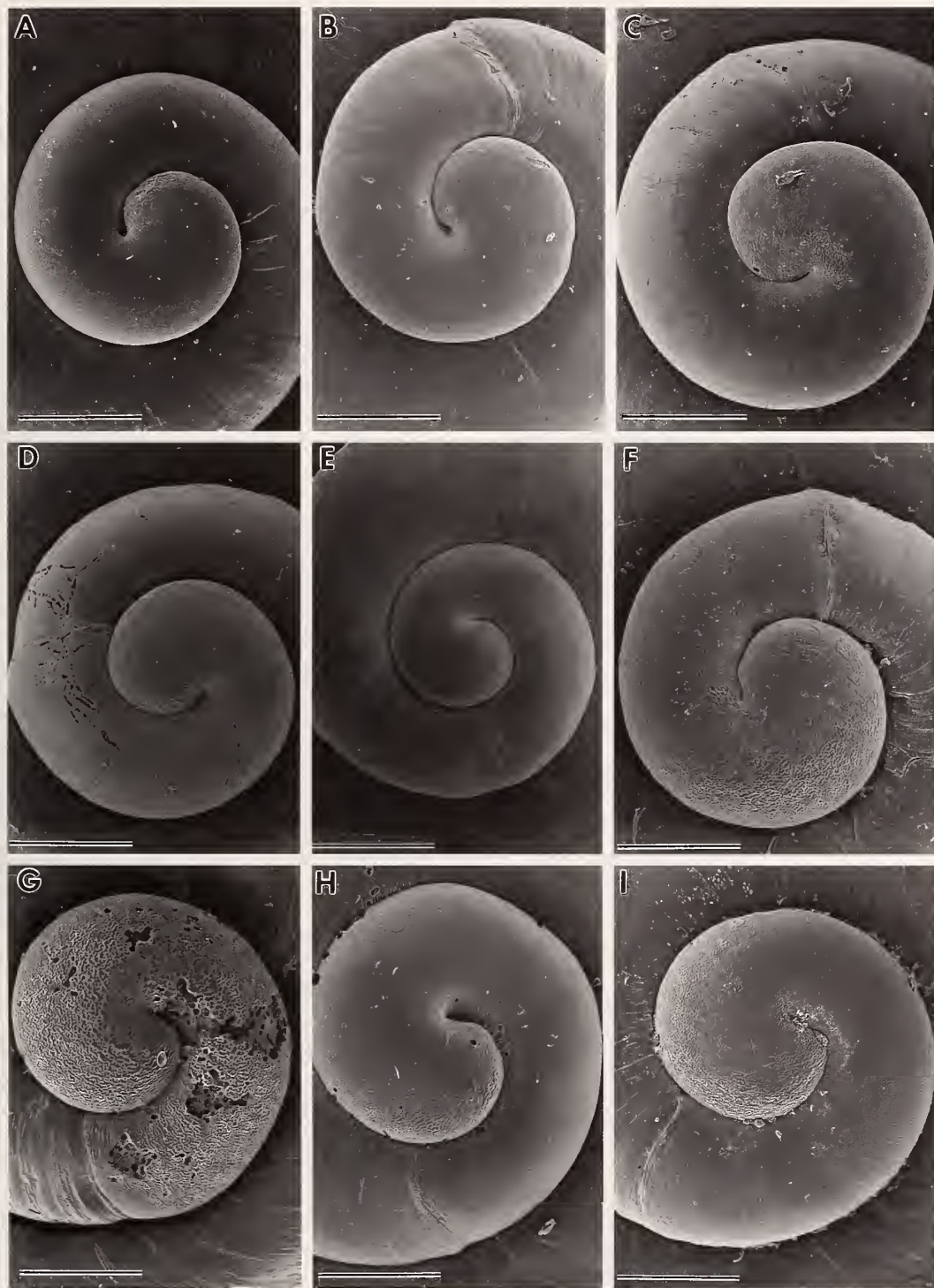
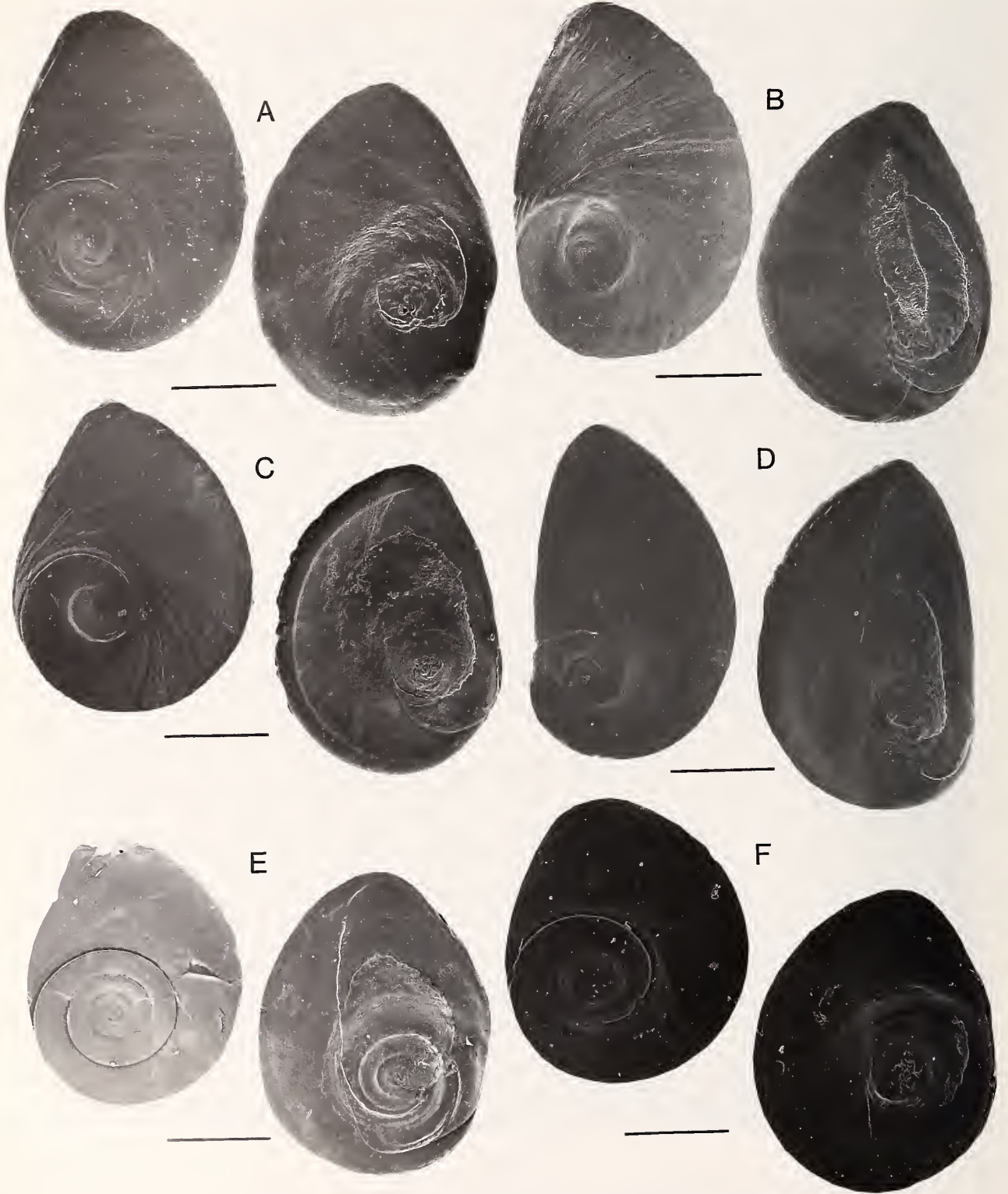


Figure 11

Shell protoconchs of *Pyrgulopsis* species. A. *P. deaconi*, USNM 860676 (bar = 0.12 mm). B. *P. montana*, USNM 860694 (bar = 0.15 mm). C. *P. breviloba*, USNM 860689 (bar = 0.11 mm). D. *P. gracilis*, USNM 860698 (bar = 0.13 mm). E. *P. papillata*, USNM 860678 (bar = 0.16 mm). F. *P. sulcata*, USNM 860683 (bar = 0.10 mm). G. *P. neritella*, USNM 860684 (bar = 0.10 mm). H. *P. saxatilis*, USNM 860726 (bar = 0.10 mm). I. *P. hovinghi*, USNM 860720 (bar = 0.11 mm).



visceral coil medium to uniform black. Ventral surface of penial filament pigmented with scattered black granules.

Ctenidial filaments 11, without pleats; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, ovate, centered slightly anterior to middle of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling 50% of digestive gland behind stomach, abutting posterior edge of stomach anteriorly. Distal female genitalia shown in Figure 26A. Albumen gland having short or no pallial component. Capsule gland shorter, narrower than albumen gland, sub-circular in section; rectal furrow weak or absent. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a single, tight circular loop. Oviduct and bursal duct joining well behind pallial wall; common duct broad, sometimes embedded in albumen gland distally. Bursa copulatrix as wide and almost as long as albumen gland, broadly ovate-pyriform, longitudinal, posterior to and pressed against edge of albumen gland. Bursal duct originating from anterior edge slightly dorsal to midline, long, narrow, but broadening distally, lying in shallow depression in albumen gland. Seminal receptacle small, narrow, overlapping anterior bursa along ventral edge, largely posterior to albumen gland.

Testis 0.75–1.0 whorl, filling more than 50% of digestive gland behind stomach, abutting posterior edge of stomach. Prostate gland large, bean-shaped, entirely visceral, narrowly ovate in section. Proximal pallial vas deferens having twist or sharp bend. Penis (Figure 26B, C) large; base nearly square, smooth; filament slightly shorter than base, broad, tapering, longitudinal; lobe shorter than filament, knoblike, longitudinal. Terminal gland short, narrow, slightly curved, sometimes divided into two units, transverse, extending onto both dorsal and ventral surfaces. Penial gland filling entire length and width of filament, slightly overlapping penis base. Dg1 short, transverse, positioned near outer edge proximal to penial gland. Dg2 dotlike, near inner edge. Dg3 long, curved, borne on low swelling. Dorsal glands sometimes accompanied by small glandular dot between Dg1 and Dg2. Ventral gland large, narrow, sometimes divided into two units, borne on low swelling, curving from near outer edge at mid-length to distal inner edge and extending to edge of lobe. Penial duct almost straight, near outer edge.

**Type locality:** Corn Creek Springs, Las Vegas Valley, Clark Country, Nevada, T. 17 S, R. 59 E, NE ¼ section

34. Corn Creek Springs lie within the Desert National Wildlife Refuge Complex (Figure 49) and comprise a main spring, now modified by a cement-lined outflow, and several smaller springs and seeps, all of which are thermal (ca. 23°C.) The type locality is a small spring several hundred meters south of the main spring. Holotype, USNM 874757 (Figure 17A), collected by D. W. Sada, 6 June 1992; paratypes, USNM 860765.

**Remarks:** Among the group of *Pyrgulopsis* having a full complement of glands on the penis, this species is distinguished by a very large penial gland (covering all of the filament) and a uniquely elongate ventral gland that crosses the entire width of the penis and extends along the inner edge of the penis distally. These features are approached in *P. deaconi* (described below), which occurs in the nearby Spring Mountains, although the terminal and ventral glands in *P. deaconi* are not as large, and the ventral gland does not extend to the inner edge as in *P. fausta*. *Pyrgulopsis fausta* is further distinguished from this species by its squatter penis with broader filament, larger penial gland, and presence of Dg1 and Dg2.

**Material examined:** NEVADA. *Clark County:* Corn Creek Springs (main spring), USNM 873183, USNM 873397, USNM 873413, USNM 873419.—Corn Creek Springs (small seep east of above), USNM 873175.—Corn Creek Springs (small spring south of main spring), USNM 860765, USNM 874757.—Corn Creek Springs, USNM 873453.

*Pyrgulopsis deaconi* Hershler, sp. nov.

Spring Mountains pyrg

(Figures 6B, 11A, 17B, C, 26D–G)

**Etymology:** Named after James Deacon (University of Nevada, Las Vegas), in recognition of his numerous studies of the spring biota of southern Nevada over the past 35 years.

**Diagnosis:** Small, with sub-globose shell. Penis large; filament medium length, lobe short. Penial ornament a small terminal gland, large penial gland, large Dg3, and large ventral gland.

**Description:** Shell (Figures 6B, 17B, C) sub-globose, width/height, 79–89%; height, 1.5–1.9 mm; width, 1.3–1.7 mm; whorls, 3.5–3.75. Protoconch (Figure 11A) 1.25 whorls, diameter 0.26 mm, initial 0.75 whorl finely wrinkled (sculpture coarser near apex), later portion nearly

Figure 12

Opercula of *Pyrgulopsis* species. A. *P. fausta*, USNM 860765 (bar = 0.26 mm). B. *P. montana*, USNM 860694 (bar = 0.26 mm). C. *P. sathos*, USNM 860691 (bar = 0.76 mm). D. *P. lata*, USNM 860697 (bar = 0.22 mm). E. *P. sublata*, USNM 860724 (bar = 0.31 mm). F. *P. lockensis*, USNM 874879 (bar = 0.28 mm).





smooth. Teleoconch whorls moderately convex, usually shouldered. Aperture broadly ovate, narrowly adnate above or slightly separated from body whorl. Inner lip slightly thickened, without columellar shelf. Outer lip usually thin, prosocline, weakly sinuate. Umbilicus rimate or perforate. Periostracum light tan.

Operculum ovate, amber; nucleus slightly eccentric; dorsal surface weakly frilled; outer margin sometimes having weak rim. Attachment scar thick all around.

Radula  $560 \times 80 \mu\text{m}$ , with 62 rows of teeth. Central tooth  $25 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 4–6; central cusp narrow, daggerlike; basal cusps small. Basal tongue narrow V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-(3-4); weakly flexed; outer wing 150–200% of cutting edge length. Inner marginal teeth with 21–22 cusps; cutting edge occupying 40% of length of tooth. Outer marginal teeth with 30–33 cusps; cutting edge occupying 16% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles unpigmented or light grey. Snout unpigmented to medium brown-grey. Foot unpigmented to medium grey. Opercular lobe having black subepithelial pigment along inner edge. Neck light grey. Pallial roof, visceral coil black. Ventral surface of penial filament having light to medium cover of black granules, pigment sometimes also present on dorsal surface alongside penial gland.

Ctenidial filaments, 14–15, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, ovate, centrally positioned. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 1.0 whorl, filling more than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 26D. Albumen gland having medium pallial component. Capsule gland shorter, narrower than albumen gland, sub-circular in section; rectal furrow absent. Ventral channel broadly overlapping capsule gland, distal end slightly separated from gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a single, tight circular loop. Oviduct and bursal duct joining well behind pallial wall; common duct broad, sometimes embedded in albumen gland distally. Bursa copulatrix as wide as albumen gland, medium width, broadly ovate to sub-circular, longitudinal, posterior to and pressed against edge of albumen

gland. Bursal duct originating from anterior edge slightly dorsal to mid-line, long, narrow, broadening distally, lying in shallow depression in albumen gland. Seminal receptacle small, ovate-narrow, overlapping anterior bursa along ventral edge posterior to albumen gland.

Testis 1.0 whorl, filling more than 50% of length of digestive gland behind stomach; overlapping posterior stomach chamber anteriorly. Prostate gland ovate, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens thick, reflexed. Penis (Figure 26E–G) large, base rectangular, sometimes weakly folded along inner edge; filament much shorter than base, medium width, tapering; lobe short, knoblike, oblique. Terminal gland short, narrow to sub-circular, sometimes slightly curved, transverse-oblique, largely on ventral surface. Penial gland filling most of filament length and width, slightly overlapping penis base. Dg3 long, borne on low swelling, sometimes flanked by small glandular dot proximally. Ventral gland large, narrow, often divided into two units, borne on low swelling, positioned between outer edge and mid-line. Penial duct near straight, near outer edge.

**Type locality:** Red Spring, Red Rock Canyon Recreation Lands, Las Vegas Valley, Clark County, Nevada, T. 21 S, R. 59 E, SW  $\frac{1}{4}$  section 6. Holotype, USNM 874454 (Figure 17B), collected by J. J. Landye, 2 January, 1992; paratypes, USNM 860676. The type locality is a small rheocene that has been moderately impacted by recreational activities.

**Remarks:** *Pyrgulopsis deaconi* is contrasted with *P. fausta* above. This species is restricted to the Spring Mountains, in drainages of Las Vegas and Pahrump Valleys (Figure 49). The population at Manse Ranch on the floor of Pahrump Valley now is extinct as the spring dried in 1975 (Soltz & Naiman, 1978:24), presumably as a result of local groundwater withdrawal (Minckley & Deacon, 1968:1429).

**Material examined:** NEVADA. *Clark County:* Red Spring, USNM 860676, USNM 873355, USNM 874084, USNM 874108, USNM 874454, USNM 874457.—Willow Spring, Las Vegas Valley, T. 20 S, R. 58 E, SW  $\frac{1}{4}$  section 33, USNM 873452, USNM 874085, USNM 874456.—Kiup Spring, Pahrump Valley, T. 20 S, R. 56 E, SE  $\frac{1}{4}$  section 31, USNM 854737, USNM 873351, USNM 874390.—*Nye County:* Spring, Manse Ranch, Pahrump Valley, T. 21 S, R. 54 E, NW  $\frac{1}{4}$  section 3, SBMNH uncat.

←

Figure 13

Opercula of *Pyrgulopsis* species. A. *P. villacampae*, USNM 860712 (bar = 0.44 mm). B. *P. planulata*, USNM 860686 (bar = 0.17 mm). C. *P. dixensis*, USNM 860688 (bar = 0.15 mm). D. *P. basiglans*, USNM 860692 (bar = 0.22 mm). E. *P. humboldtensis*, USNM 860718 (bar = 0.31 mm). F. *P. plicata*, USNM 860727 (bar = 0.28 mm).



Figure 14

Radulae of *Pyrgulopsis* species. A-C. *P. hubbsi*, USNM 874776 (bars = 22  $\mu$ m, 24  $\mu$ m, 67  $\mu$ m, respectively). D-F. *P. breviloba*, USNM 860689 (bars = 11  $\mu$ m, 17  $\mu$ m, 46  $\mu$ m, respectively). G-I. *P. lockensis*, USNM 874879 (bars = 14  $\mu$ m, 14  $\mu$ m, 35  $\mu$ m, respectively). Photographs show (from left to right) central teeth, lateral teeth, and general view of portion of radula ribbon.

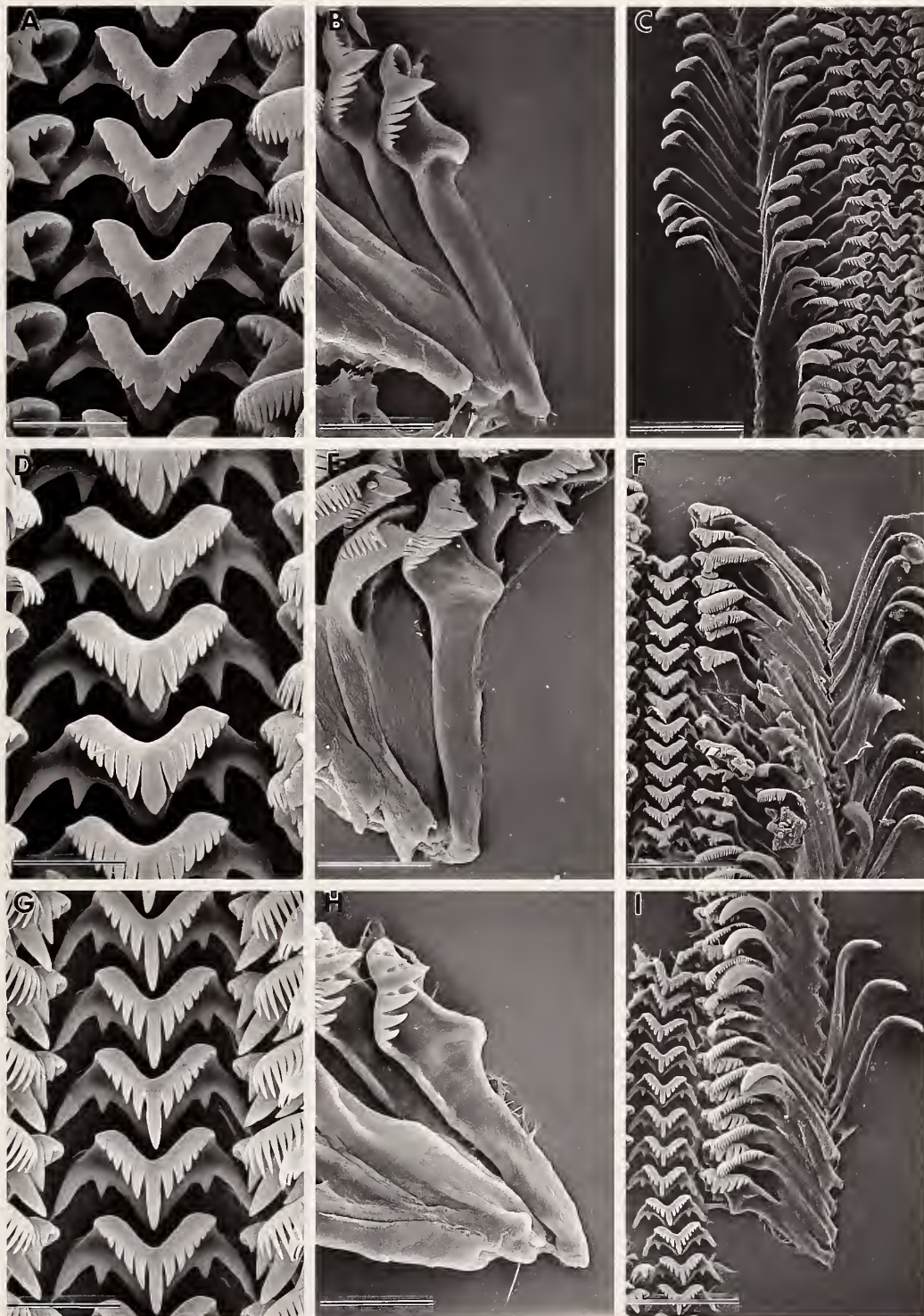


Figure 15

Radulae of *Pyrgulopsis* species. A–C. *P. planulata*, USNM 860686 (bars = 8  $\mu$ m, 12  $\mu$ m, 43  $\mu$ m, respectively). D–F. *P. serrata*, USNM 860719 (bars = 8  $\mu$ m, 13  $\mu$ m, 38  $\mu$ m, respectively). G–I. *P. militaris*, USNM 860704 (bars = 10  $\mu$ m, 13  $\mu$ m, 33  $\mu$ m, respectively). Photographs show (from left to right) central teeth, lateral teeth, and general view of portion of radula ribbon.

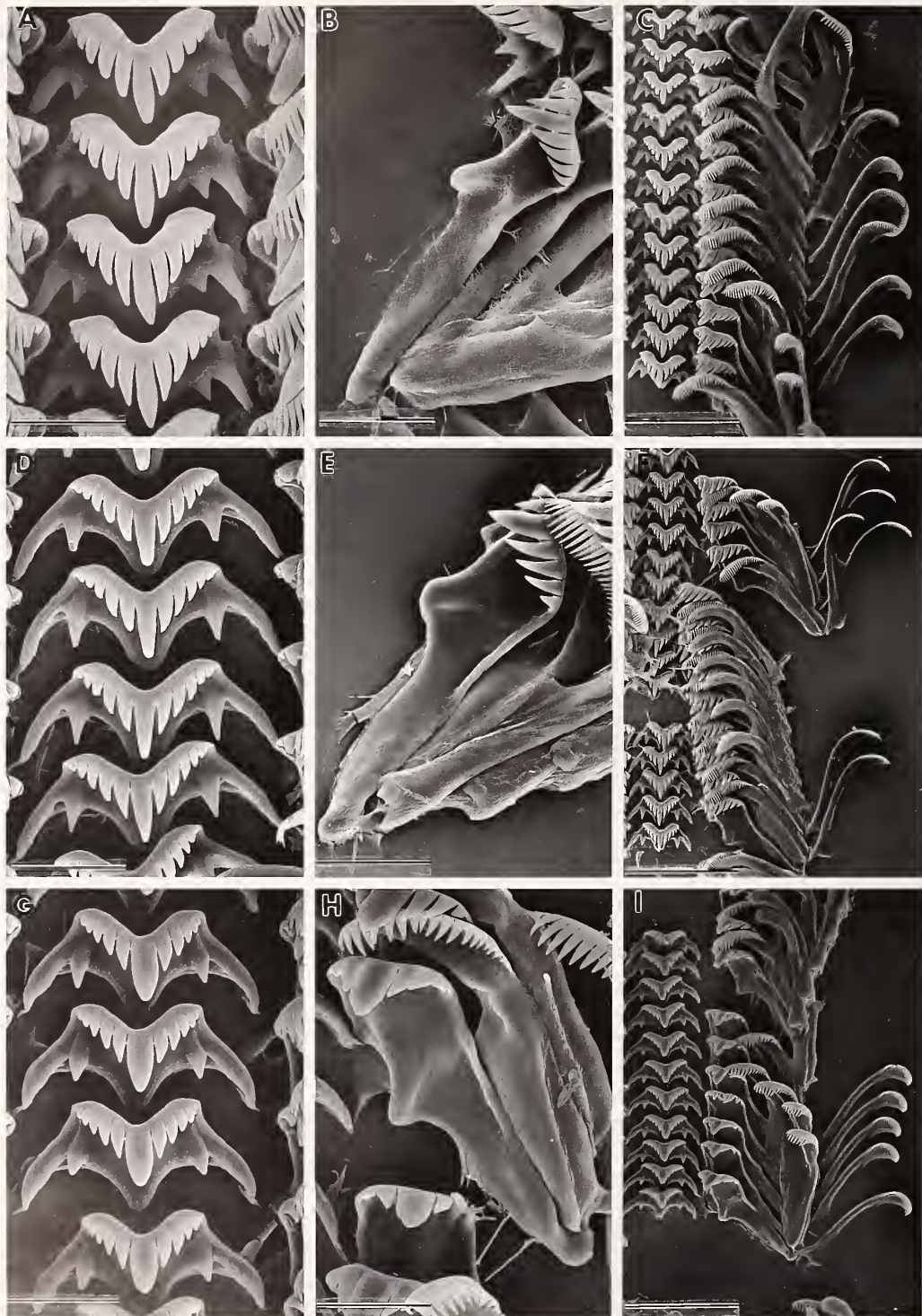


Figure 16

Radulae of *Pyrgulopsis* species. A–C. *P. saxatilis*, USNM 860726 (bars = 8  $\mu$ m, 10  $\mu$ m, 24  $\mu$ m, respectively). D–F *P. hovinghi*, USNM 874715 (bars = 11  $\mu$ m, 15  $\mu$ m, 46  $\mu$ m, respectively). G–I. *P. transversa*, USNM 860732 (bars = 13  $\mu$ m, 14  $\mu$ m, 41  $\mu$ m, respectively). Photographs show (from left to right) central teeth, lateral teeth, and general view of portion of radula ribbon.

*Pyrgulopsis coloradensis* Hershler, sp. nov.

## Blue Point pyrg

(Figures 6C, 17D, 27A, B)

**Etymology:** The species name refers to the occurrence of this snail in Colorado River drainage.

**Diagnosis:** Small, with low trochoid to ovate-conic shell. Penis medium-sized, bladelike, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 6C, 17D) sub-globose to ovate-conic, width/height, 80–93%; height, 1.2–1.6 mm; width, 1.0–1.3 mm; whorls, 2.75–3.5. Protoconch 1.25 whorls, diameter 0.29 mm, initial 0.75 whorl having well-developed wrinkles, sculpture weakening, becoming near smooth on later portion. Teleoconch whorls medium to highly convex, shouldered. Aperture ovate, usually well separated from body whorl. Inner lip often thick, without columellar shelf. Outer lip slightly thickened, orthocone, without sinuation. Umbilicus perforate, umbilical region sometimes excavated and having weak adaxial ridge. Periostracum light tan.

Operculum ovate, amber, nuclear region reddish; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar slightly thickened all around.

Radula 460 × 64 μm, with 66 rows of teeth. Central tooth 16 μm wide, broad, with medium indented dorsal edge; lateral cusps 5–7; central cusp narrow, distally rounded; basal cusps small. Basal tongue broad V-shaped, sockets medium. Lateral tooth formula 4-1-4(5); neck weakly flexed; outer wing 225% of cutting edge length. Inner marginal teeth with 21–25 cusps; cutting edge occupying 30% of length of tooth. Outer marginal teeth with 23–28 cusps; cutting edge occupying 27% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal in size; stomach caecum very small.

Cephalic tentacles medium to dark brown or black. Snout dark brown or black. Sides of foot dark grey or brown; opercular lobe dark along inner edge, sometimes pigmented all around. Neck medium to dark brown or black. Pallial roof, visceral coil uniformly black. Dorsal surface of penial filament having few, scattered black granules distally.

Ctenidial filaments 14, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium medium-sized, narrowly ovate, positioned alongside posterior half of ctenidium. Renal gland horizontal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior and sometimes portion of anterior stomach chambers. Distal female genitalia shown in Figure 27A. Albumen gland without pallial component. Capsule gland slightly longer, but narrower than albumen gland, broadly ovate in section; rectal furrow absent. Ventral channel slightly overlapping cap-

sule gland; longitudinal fold weakly developed. Genital aperture a terminal slit without anterior extension. Coiled oviduct a tight circular loop sometimes preceded by slight twist. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, narrow, clublike, longitudinal, 50% of length posterior to albumen gland. Bursal duct originating from anterior edge, as long as, slightly narrower than bursa. Seminal receptacle medium-sized, narrow, often folded, partly overlapping ventral edge of bursa, extending almost to edge of albumen gland.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers and extending to edge of prostate gland. Prostate gland fat bean-shaped, pallial portion large (slightly less than 50%), ovate in section. Proximal pallial vas deferens reflexed. Penis (Figure 27B) medium-sized; gently tapering, base and filament poorly differentiated; inner edge weakly folded or smooth; lobe and glands absent. Penial duct near straight, near outer edge.

**Type locality:** Blue Point Spring, Colorado River drainage, Clark County, Nevada, T. 18 S, R. 68 E, SW ¼ section 6 (Figure 49). Holotype, USNM 854621 (Figure 17D), collected by R. Hershler, 10 October 1993; paratypes USNM 860677. *Pyrgulopsis coloradensis* occurs in limited abundance (having become increasingly scarce in the past decade) in this small, thermal (30°C.) rheocrone, which is situated within the Lake Mead National Recreation Area.

**Remarks:** This isolated local endemic differs from the group of simple-pened species in Railroad Valley by its more elongate shell; simply tapering, smooth penis; and small, narrow bursa copulatrix.

**Material examined:** NEVADA. *Clark County:* Blue Point Spring, USNM 854621, USNM 854641, USNM 860677, USNM 873347, USNM 873360.

*Pyrgulopsis avernalis* (Pilsbry, 1935)

*Fluminicola avernalis* Pilsbry, 1935:92, fig. 1.—Williams et al., 1985:48 [habitat notes].

“*Fluminicola*” *avernalis* (Pilsbry, 1935), Taylor, 1975:40 [literature compilation].—Pratt, 1977:7 [habitat notes].—Taylor, 1983:294 [Miocene Muddy Creek Formation, Clark County, Nevada].

*Pyrgulopsis avernalis* (Pilsbry, 1935), Hershler, 1994:19, 21 [figures; transfer to *Pyrgulopsis*].

**Diagnosis:** Medium-sized, with globose-trochoid shell. Penis large, filament short, lobe absent. Penial ornament a large ventral gland.

**Type locality:** Colorado Desert (fossil); emended to Moapa Valley (southern Nevada) by Hershler (1994:19).

**Remarks:** All material collected during this survey was from the type locality area in Moapa Valley (Figure 49).

**Material examined:** NEVADA. *Clark County:* Spring,



Moapa National Wildlife Refuge, Moapa Valley, T. 14 S, R. 65 E, NE ¼ section 21, USNM 873454, USNM 874088, USNM 874344.—“Apcar Springs,” Moapa Valley, T. 14 S, R. 65 E, SE ¼ section 16, USNM 874000, USNM 874014.—“Cardy Lamb Spring,” Moapa Valley, T. 14 S, R. 65 E, SW ¼ section 16, USNM 874353, USNM 874354, USNM 874780, USNM 874781.—Springs, west of Muddy Spring, Moapa Valley, T. 14 S, R. 65 E, NW ¼ section 16, USNM 874003, USNM 874005, USNM 874015, USNM 874082, USNM 874089.—Muddy Spring, T. 14 S, R. 65 E, NE ¼ section 16, USNM 874110, USNM 874347.

*Pyrgulopsis carinifera* (Pilsbry, 1935)

*Fluminicola avernalis carinifera* Pilsbry, 1935:93, fig. 3.  
 “*Fluminicola*” *carinifera* Pilsbry, 1935, Taylor, 1975:53 [literature compilation].  
 “Undescribed species of *Fontelicella*” Pratt, 1977:7 [habitat notes].  
*Pyrgulopsis carinifera* (Pilsbry, 1935), Hershler, 1994:26–27 [figures; transfer to *Pyrgulopsis*; elevation to full species status].

**Diagnosis:** Medium-sized, with trochoid shell. Penis medium-sized; filament medium length, lobe medium length. Penial ornament a large, fragmented terminal gland.

**Type locality:** Colorado Desert (fossil); emended to Moapa Valley (southern Nevada) by Hershler (1994:19).

**Remarks:** All material collected during this survey was from the type locality area in Moapa Valley (Figure 49).

**Material examined:** NEVADA. *Clark County*: Spring, Moapa National Wildlife Refuge, Moapa Valley, T. 14 S, R. 65 E, NE ¼ section 21, USNM 873475, USNM 874083, USNM 874097, USNM 874098, USNM 874507, USNM 874784, USNM 874785.—“Apcar Springs,” Moapa Valley, T. 14 S, R. 65 E, SE ¼ section 16, USNM 874001, USNM 874004, USNM 874348.—Springs, west of Muddy Spring, Moapa Valley, T. 14 S, R. 65 E, NW ¼ section 16, USNM 874350.—Muddy Spring, T. 14 S, R. 65 E, NE ¼ section 16, USNM 874099, USNM 874111, USNM 874345, USNM 874786, USNM 874791.

*Pyrgulopsis merriami* (Pilsbry & Beecher, 1892)

*Fluminicola merriami* Pilsbry & Beecher in Pilsbry, 1892: 143.–Williams et al., 1985:36 [in part; habitat notes].

“*Fluminicola*” *merriami* Pilsbry & Beecher in Pilsbry, 1892, Taylor, 1975:122 [literature compilation].  
*Pyrgulopsis merriami* (Pilsbry and Beecher in Pilsbry, 1892), Hershler, 1994:49 [figures; transfer to *Pyrgulopsis*].

**Diagnosis:** Medium-sized, with globose shell. Penis large, filament short, lobe medium length. Penial ornament a small terminal gland, large, trifold, penial gland; small Dg3, and large ventral gland.

**Type locality:** A warm spring in Pahranaagat Valley, Nevada.

**Remarks:** This species occupies much of the upper course of the pluvial White River (Figure 49). Populations from the White River Valley differ from those of Pahranaagat Valley in that the ventral gland of the penis is borne on a long stalk.

**Material examined:** NEVADA. *Nye County*: Hot Creek Spring, White River Valley, T. 6 N, R. 61 E, NE ¼ section 18, USNM 873159, USNM 874013, USNM 874689.—Moon River Spring, White River Valley, T. 6 N, R. 60 E, NE ¼ section 25, USNM 874677.—Moorman Spring, White River Valley, T. 8 N, R. 61 E, SE ¼ section 32, USNM 873190, USNM 874684.

*Pyrgulopsis montana* Hershler, sp. nov.

Camp Valley pyrg

(Figures 6D, 11B, 12B, 17E, 27C–E)

**Etymology:** From *montanus* (Latin), of mountains; referring to the montane habitat of this species.

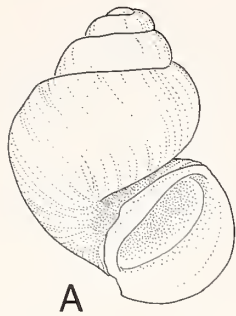
**Diagnosis:** Medium-sized, with sub-globose to ovate-conic shell. Penis small, filament medium length, lobe short. Penial ornament a small terminal gland.

**Description:** Shell (Figures 6D, 17E) sub-globose to ovate-conic, width/height, 70–82%; height, 2.1–3.0 mm; width, 1.6–2.1 mm; whorls, 3.25–4.0. Protoconch (Figure 11B) 1.2 whorls, diameter 0.28 mm, smooth. Teleoconch whorls highly convex, sometimes having narrow shoulders. Aperture ovate, narrowly adnate or slightly separated from body whorl. Inner lip slightly thickened, without columellar shelf. Outer lip slightly thickened, weakly prosocline, without sinuation. Umbilicus perforate. Periostracum light brown.

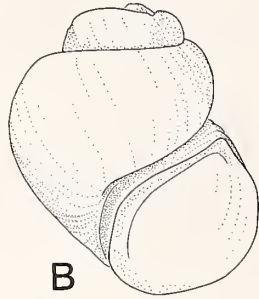
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Figure 17

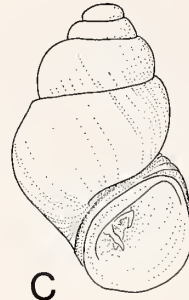
Shells of *Pyrgulopsis* species. A. *P. fausta*, holotype, USNM 874757 (shell height, 1.6 mm). B. *P. deaconi*, holotype, USNM 874454 (1.9 mm). C. *P. deaconi*, USNM 854737 (1.7 mm). D. *P. coloradensis*, holotype, USNM 854621 (1.2 mm). E. *P. montana*, holotype, USNM 874686 (1.8 mm). F. *P. hubbsi*, holotype, USNM 873415 (3.6 mm). G. *P. hubbsi*, USNM 873405 (3.0 mm). H. *P. sathos*, holotype, USNM 874664 (3.6 mm). I. *P. sathos*, USNM 874663 (2.1 mm). J. *P. sathos*, USNM 873198 (4.3 mm). K. *P. sathos*, USNM 883852 (4.2 mm). L. *P. breviloba*, holotype, USNM 873174 (1.9 mm). M. *P. breviloba*, USNM 874671 (1.3 mm).



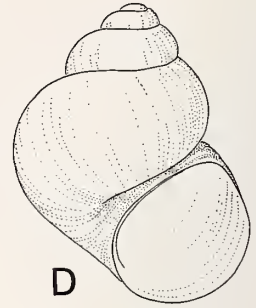
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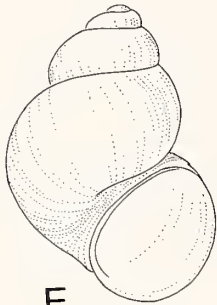
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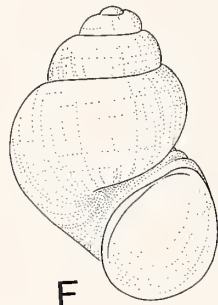
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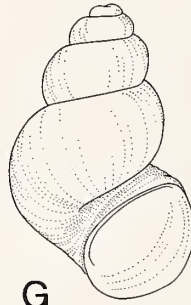
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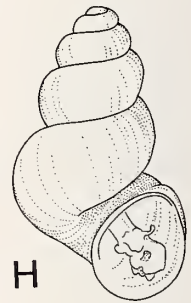
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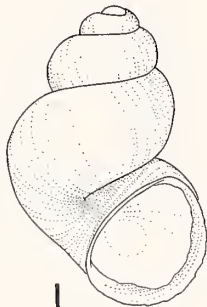
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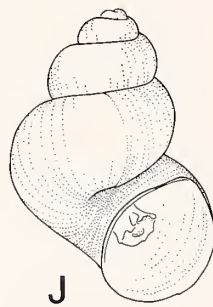
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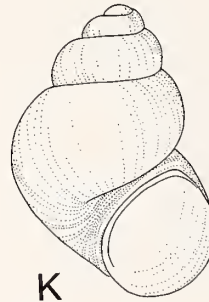
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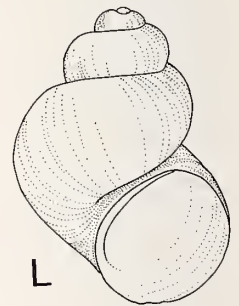
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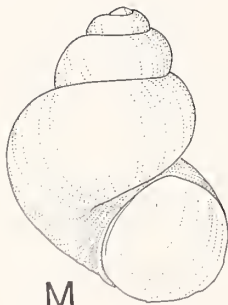
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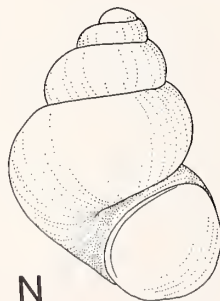
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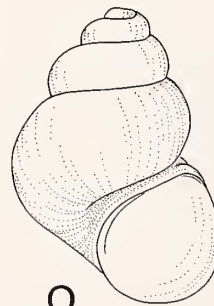
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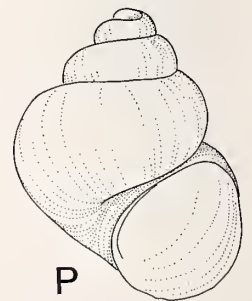
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Operculum (Figure 12B) ovate, dark amber, nuclear region reddish; nucleus eccentric; dorsal surface smooth; outer margin having weak rim. Attachment scar margin thick between nucleus and inner edge.

Radula  $630 \times 108 \mu\text{m}$ , with 55 rows of teeth. Central tooth  $23 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 6–7; central cusp narrow, daggerlike; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-4(5); neck medium flexed; outer wing 150% of cutting edge length. Inner marginal teeth with 27–30 cusps; cutting edge occupying 33% of tooth length. Outer marginal teeth with 30–31 cusps; cutting edge occupying 24% of tooth length. Stomach slightly longer than style sac; stomach chambers equal in size; stomach caecum very small.

Cephalic tentacles, snout, neck light to dark grey-brown. Foot light to dark grey, pigment heaviest along anterior and posterior margins. Opercular lobe medium to dark grey, pigment heaviest along inner edge and sides. Pallial roof, visceral coil near uniform medium to dark brown-grey or black. Dark internal pigment filling most of penial filament and portion of proximal penis; lobe also sometimes having scattered black pigment.

Ctenidial filaments, 17, pleated; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland longitudinal-slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, abutting prostate gland.

Ovary 0.5–0.75 whorl, filling 50% of digestive gland behind stomach, overlapping both stomach chambers. Distal female genitalia shown in Figure 27C. Albumen gland having medium pallial component. Capsule gland shorter, slightly narrower than albumen gland, broadly ovate in section; rectal furrow weakly developed. Ventral channel moderately overlapping capsule gland; longitudinal fold moderately developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a tight circular loop usually preceded by weak twist. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix medium length and width, narrow-ovate, often having silvery appearance, longitudinal or oblique, positioned along postero-ventral edge of albumen gland, with small portion extending posterior to gland. Bursal duct originating from anterior edge at mid-line, long, me-

dium width, broadening distally. Seminal receptacle small, pouchlike, overlapping or abutting proximal portion of bursal duct close to ventral edge of albumen gland.

Testis 1.25–1.5 whorls, filling 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland small, broadly ovate, entirely visceral or having short pallial portion, narrowly ovate in section. Proximal pallial vas deferens straight or with weak undulation. Penis (Figure 27D, E) small; base rectangular to near square, strongly folded; filament slightly shorter than base, broad, tapering to sharp point, longitudinal; lobe short, knoblike, longitudinal. Terminal gland short, narrow-circular, sometimes longitudinal, ventral. Penial duct straight, near outer edge.

**Type locality:** Spring, upper Camp Valley, Lincoln County, Nevada, T. 5 N, R. 69 E, center section 8 (Figure 49). Holotype, USNM 874686 (Figure 17E), collected by R. Hershler and P. Hovingh, 24 June 1992; paratypes, USNM 860694. The type locality is a small rheocrene heavily impacted by cattle.

**Remarks:** This species closely resembles *P. hamlinensis* (described below), which occurs to the east in the Bonneville Basin, as both species share a smooth protoconch and relatively simple penis ornamented solely by a terminal gland. *Pyrgulopsis montana* differs from this species in its slightly broader shell with simple whorl outline, and weaker operculum attachment scar.

**Material examined:** NEVADA. *Lincoln County:* Spring, upper Camp Valley, USNM 860694, USNM 874686.

*Pyrgulopsis hubbsi* Hershler, sp. nov.

Hubbs pyrg

(Figures 6E, 14A–C, 17F, G, 27F–H)

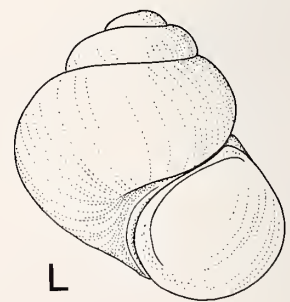
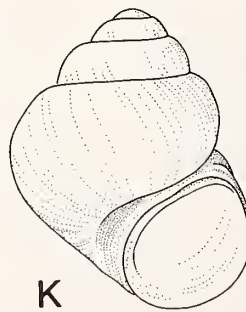
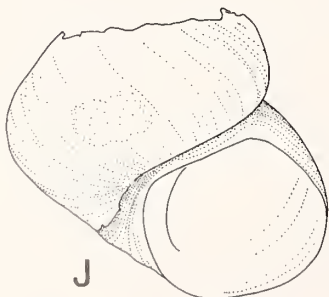
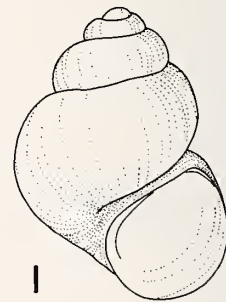
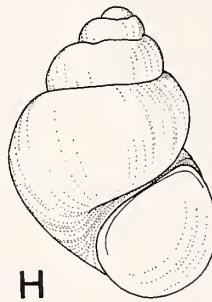
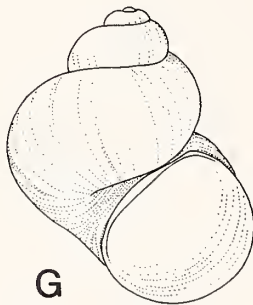
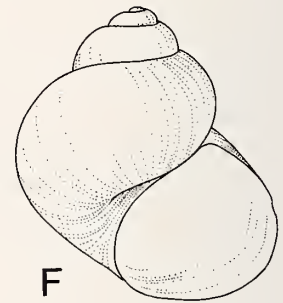
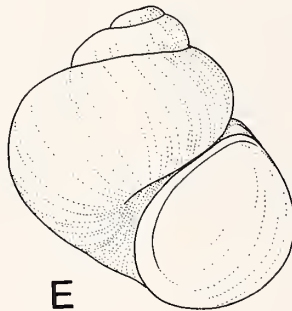
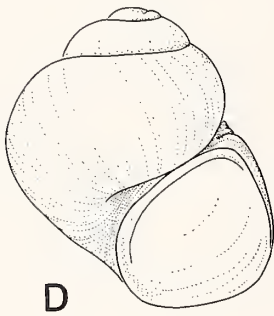
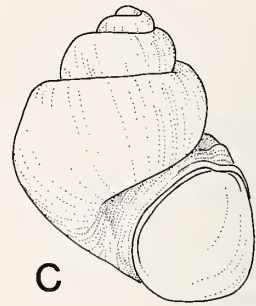
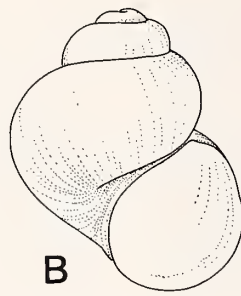
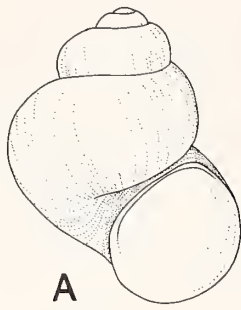
**Etymology:** Named after the late Carl Hubbs, in recognition of his extensive contributions to the study of fishes and drainage history of the Great Basin.

**Diagnosis:** Medium-sized to large, with globose to low-conical shell. Penis medium-sized, filament long, lobe short. Penial ornament a dotlike terminal gland.

**Description:** Shell (Figures 6E, 17F, G) globose to low-conical, apex usually eroded, width/height, 82–95%;

Figure 18

Shells of *Pyrgulopsis* species. A. *P. lata*, holotype, USNM 874667 (shell height, 1.9 mm). B. *P. gracilis*, holotype, USNM 873158 (2.0 mm). C. *P. gracilis*, USNM 883885 (2.1 mm). D. *P. marcida*, holotype, USNM 873154 (3.3 mm). E. *P. marcida*, USNM 874682 (3.9 mm). F. *P. marcida*, USNM 873170 (2.5 mm). G. *P. turbatrix*, holotype, USNM 883978 (2.9 mm). H. *P. turbatrix*, USNM 854738 (3.4 mm). I. *P. turbatrix*, USNM 874455 (2.5 mm). J. *P. turbatrix*, USNM 874775 (3.1 mm). K. *P. sterilis*, holotype, USNM 874876 (3.1 mm). L. *P. sterilis*, USNM 874769 (2.6 mm). M. *P. ruinosa*, holotype, USNM 873407 (2.6 mm). N. *P. sublata*, holotype, USNM 874681 (2.9 mm). O, P. *P. sublata*, USNM 860724 (2.2 mm, 2.4 mm, respectively).



height, 2.5–3.8 mm; width, 2.2–3.4 mm; whorls, 3.25–3.75. Protoconch 1.3 whorls, diameter 0.33 mm, initial 0.25 whorl finely wrinkled, later portion near smooth. Teleoconch whorls moderately convex, shoulders absent to well developed. Aperture broad, crescentlike, often strongly angled above; adnate or, less commonly, slightly disjunct. Inner lip thick, with medium width columellar shelf. Outer lip thick in larger specimens, prosocline, weakly sinuate. Umbilicus absent or rimate; umbilical region often weakly excavated with slight adaxial ridge. Periostracum light brown, thick.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled, outer margin having weak rim. Attachment scar slightly thickened between nucleus and inner edge.

Radula (Figure 14A–C)  $1.19 \times 140 \mu\text{m}$ , with 78 rows of teeth. Central tooth  $40 \mu\text{m}$  wide, with slightly indented dorsal edge; lateral cusps, 4–6; central cusp long, medium width, daggerlike; basal cusps small. Basal tongue broad, nearly U-shaped, considerably shorter than lateral margins; basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck medium flexed; outer wing broad, 110% of cutting edge length. Inner marginal teeth with 21–24 cusps; cutting edge occupying 29% of length of tooth. Outer marginal teeth with 30–31 cusps; cutting edge occupying 30% of length of tooth. Stomach and style sac equal-sized; anterior and posterior stomach chambers equal-sized; stomach caecum absent or very small.

Cephalic tentacles light to dark brown, usually lighter centrally and around eyespots. Snout light to dark brown, usually darker than tentacles. Foot light to dark brown. Opercular lobe unpigmented to dark along inner edge and sides. Neck light to medium brown. Pallial roof, visceral coil nearly uniform dark brown-black. Penial filament darkly pigmented internally for entire length except distalmost portion; pigment extending into distal portion of base.

Ctenidial filaments, 30, pleated, ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centrally positioned. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.75–1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior and an-

terior stomach and extending to edge of albumen gland. Distal female genitalia shown in Figure 27F. Albumen gland having short pallial component. Capsule gland slightly shorter and narrower than albumen gland, sub-circular in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland, longitudinal fold weakly developed. Genital aperture a terminal slit with short anterior extension. Coiled oviduct a tight circular loop preceded and overlapped by posterior arched kink or twist. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, medium width; sub-globular to broadly ovate, longitudinal, with 50–75% of length posterior to gland, anteriormost portion usually embedded in gland. Bursal duct originating from anterior edge at mid-line, long, narrow, embedded in albumen gland except for distalmost portion. Seminal receptacle small, pouchlike, positioned well anterior to bursa near ventral edge of albumen gland.

Testis 1.0 whorl, filling almost all of digestive gland behind stomach, overlapping anterior and posterior stomach chambers and extending to edge of prostate gland. Prostate gland very small, broadly ovate, entirely visceral or with short pallial component, narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 27G, H) medium-sized; base rectangular, weakly folded along inner edge; filament as long or slightly longer than base, broad, tapering, longitudinal; lobe very short, bud-like, longitudinal. Terminal gland dotlike, circular, sometimes divided into two units, ventral. Penial duct weakly undulating in base, straight in filament, near outer edge.

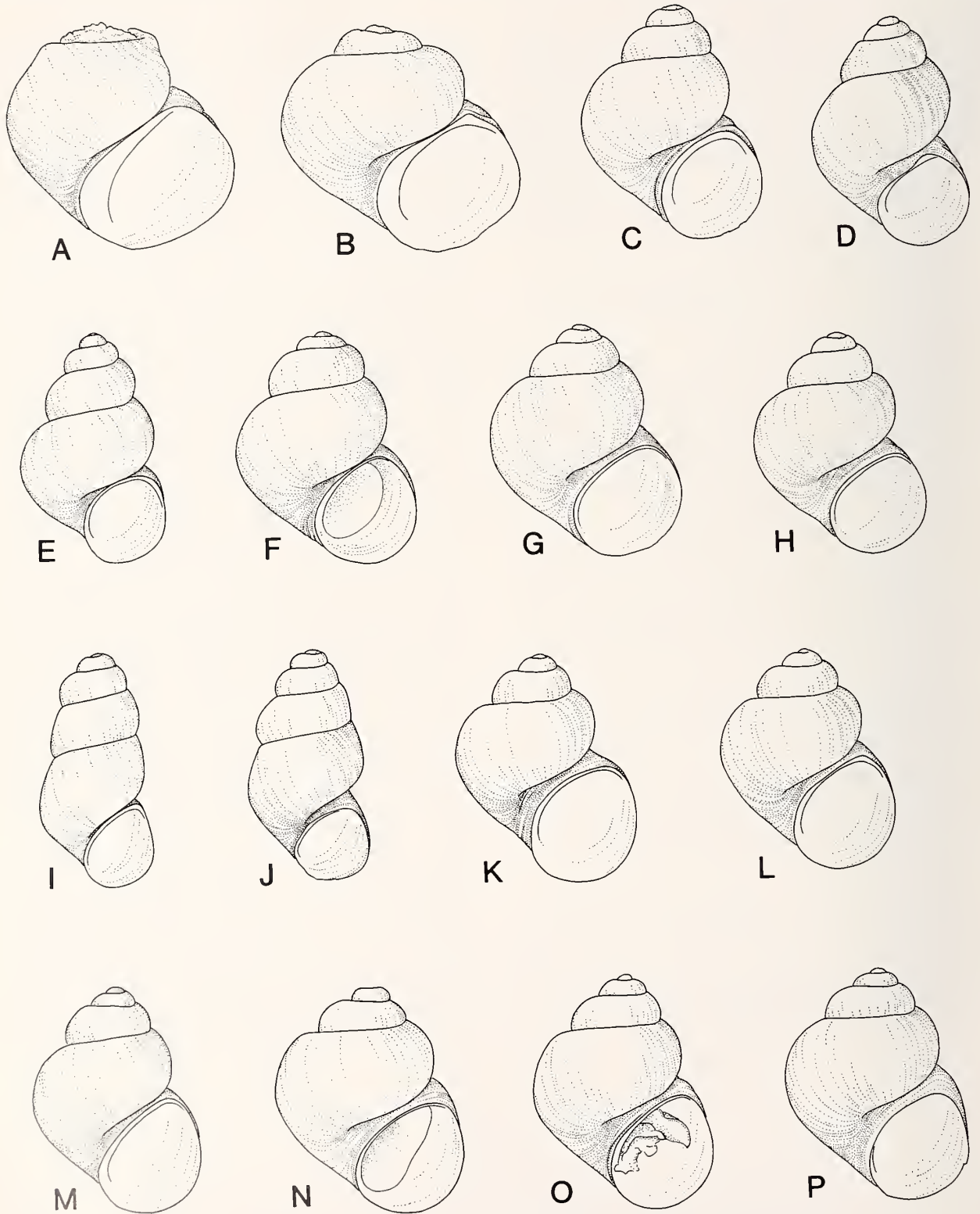
**Type locality:** Hiko Spring, Pahrangat Valley, Lincoln County, Nevada, T. 4 S, R. 60 E, SE  $\frac{1}{4}$  section 14. Holotype, USNM 873415 (Figure 17F), collected by R. Hershler, 9 July 1986; paratypes, USNM 860690. The type locality is a large, thermal (27°C.) rheocene.

**Remarks:** *Pyrgulopsis hubbsi* resembles *P. sathos* (described next), from White River Valley, in having weak protoconch sculpture; short, broad lateral wings on the lateral marginal teeth; ovate bursa copulatrix with long duct; very small, anteriorly positioned seminal receptacle; and penis with enlarged filament, very small penial lobe, and small terminal gland. *Pyrgulopsis hubbsi* differs from this species in having a squatter shell, and lacking a ven-

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Figure 19

Shells of *Pyrgulopsis* species. A. *P. lockensis*, holotype, USNM 874779 (shell height, 2.0 mm). B. *P. papillata*, holotype, USNM 873185 (2.1 mm). C. *P. carinata*, holotype, USNM 883975 (2.2 mm). D. *P. aloba*, holotype, USNM 883847 (1.1 mm). E. *P. aloba*, USNM 873187 (1.3 mm). F. *P. villacampae*, holotype, USNM 873191 (2.6 mm). G. *P. villacampae*, USNM 883938 (3.6 mm). H. *P. anatina*, holotype, USNM 883848 (2.8 mm). I. *P. anatina*, USNM 860710 (2.5 mm). J. *P. planulata*, holotype, USNM 892023 (1.2 mm). K. *P. sulcata*, holotype, USNM 874326 (1.6 mm). L. *P. orbiculata*, holotype, USNM 873196 (1.3 mm).



tral gland on the penis. Distribution of *P. hubbsi* is shown in Figure 49.

**Material examined:** NEVADA. *Lincoln County*: Hiko Spring, USNM 860690, USNM 873166, USNM 873399, USNM 873415, USNM 874776.—Crystal Spring, Pahrana-gat Valley, T. 5 S, R. 60 E, NE ¼ section 10, USNM 873173, USNM 873404, USNM 873405, USNM 874081, USNM 874770.

*Pyrgulopsis sathos* Hershler, sp. nov.

White River Valley pyrg

(Figures 6F, 12C, 17H–K, 28A–C)

**Etymology:** From *sathon* (Greek), one with large penis; referring to the enlarged penial filament characterizing this species.

**Diagnosis:** Usually large, with ovate to narrow-conic shell. Penis medium-sized, filament long, lobe short. Penial ornament of small terminal and ventral glands.

**Description:** Shell (Figures 6F, 17H–K) ovate- to narrow-conic, width/height, 67–91%; height, 1.4–4.6 mm; width, 1.2–3.5 mm; whorls, 3.25–5.25. Protoconch 1.25 whorls, diameter 0.33 mm, weakly wrinkled along inner edge at apex, otherwise smooth. Teleoconch whorls medium to highly convex; shoulders absent or narrow. Aperture ovate, narrow adnate or slightly separated from body whorl. Inner lip slightly thickened, sometimes having very narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus perforate. Periostracum tan-brown.

Operculum (Figure 12C) ovate, reddish; nucleus slightly eccentric; dorsal surface weakly frilled; outer margin having well-developed rim. Attachment scar thick almost all around (except for section along outer edge).

Radula 890 × 150 μm, with 56 rows of teeth. Central tooth 39 μm wide, with slightly indented dorsal edge; lateral cusps, 4–5, central cusp medium width, dagger-like; basal cusps medium-sized, sometimes accompanied by vestige of second, outer cusp. Basal tongue broad V-shaped, shorter than lateral margins, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck medium flexed; outer wing 150–170% of cutting edge length, broad. Inner marginal teeth with 21–26 cusps; cutting

edge occupying 36% of length of tooth. Outer marginal teeth with 31–35 cusps; cutting edge occupying 25% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum medium-sized.

Cephalic tentacles unpigmented to dark brown. Snout, foot light to dark brown. Opercular lobe usually dark along sides and inner edge. Neck unpigmented to medium brown. Pallial roof, visceral coil near uniform dark brown-black. Penial filament darkly pigmented internally along almost entire length.

Ctenidial filaments, 20, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered slightly posterior to middle of ctenidium. Renal gland strongly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

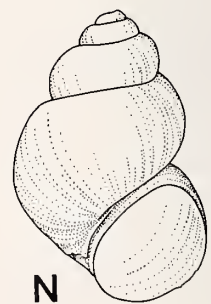
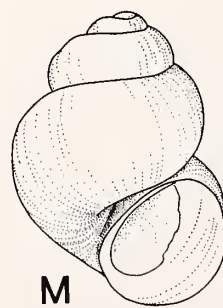
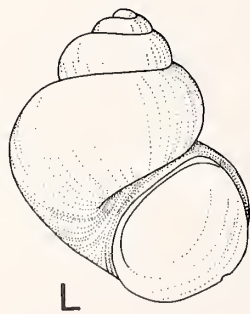
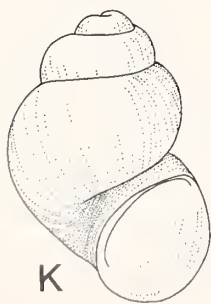
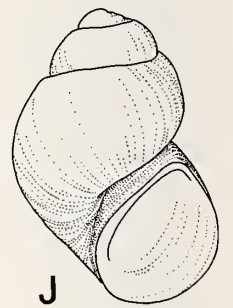
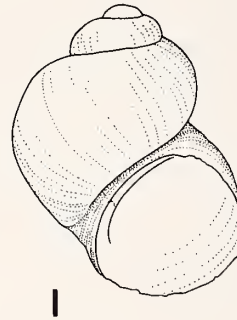
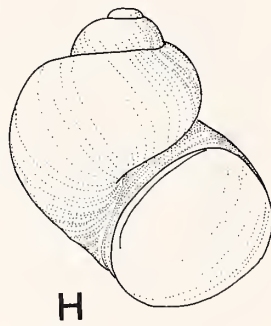
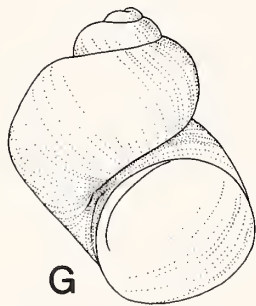
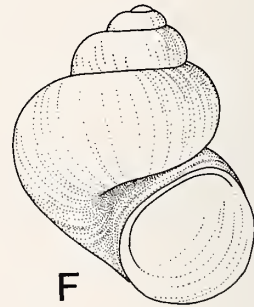
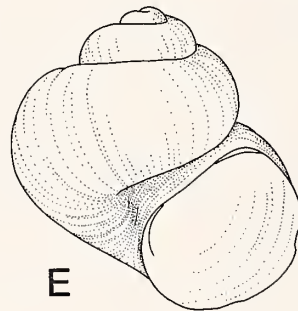
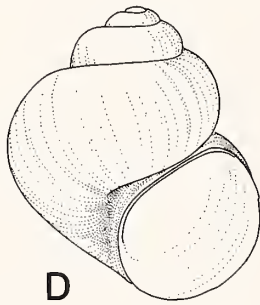
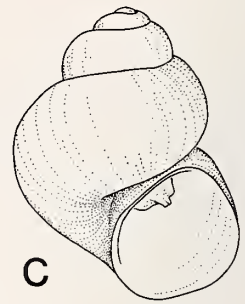
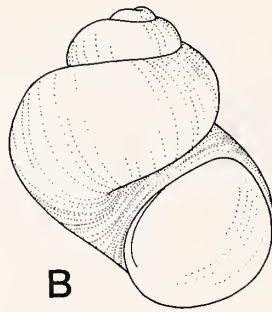
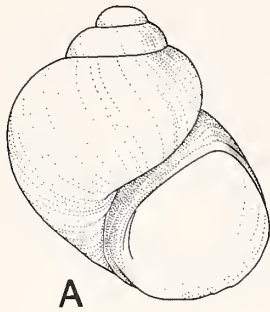
Ovary 0.75 whorl, filling 50% of digestive gland behind stomach, abutting or very slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 28A. Albumen gland having short pallial component. Capsule gland shorter and narrower than albumen gland, ovate in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes slightly raised and papillalike, with short anterior extension. Coiled oviduct of two small, overlapping posterior loops. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, slightly narrower than albumen gland, ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge of bursa at mid-line, as long or slightly shorter than bursa, ventral edge sometimes embedded in albumen gland. Seminal receptacle very small, pouchlike, positioned well anterior to bursa near ventral edge of albumen gland.

Testis 2.0 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland bean-shaped, with short pallial portion, narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 28B, C) medium-sized; base rectangular, sometimes weakly folded along inner edge basally; filament as long or longer than base, broad, tapering to point, slightly oblique; lobe short, knoblike (sometimes quite narrow), oblique. Terminal gland short, sub-circular, transverse, ventral. Ventral

←

Figure 20

Shells of *Pyrgulopsis* species. A. *P. neritella*, holotype, USNM 883932 (shell height, 1.3 mm). B. *P. landyei*, holotype, USNM 892014 (1.4 mm). C. *P. serrata*, holotype, USNM 874314 (2.2 mm). D. *P. serrata*, USNM 874318 (2.5 mm). E. *P. serrata*, USNM 874312 (3.3 mm). F. *P. cruciglans*, holotype, USNM 874285 (1.9 mm). G. *P. cruciglans*, USNM 874335 (2.3 mm). H. *P. cruciglans*, USNM 874331 (2.2 mm). I. *P. dixensis*, holotype, USNM 874391 (1.8 mm). J. *P. dixensis*, USNM 860688 (1.8 mm). K. *P. aurata*, holotype, USNM 874393 (2.7 mm). L. *P. aurata*, USNM 860696 (2.4 mm). M. *P. longiglans*, holotype, USNM 873409 (2.3 mm). N. *P. longiglans*, USNM 883451 (1.4 mm). O. *P. longiglans*, USNM 883436 (2.1 mm). P. *P. longiglans*, USNM 874293 (2.0 mm).



gland similarly small and circular; borne on swelling, sometimes pronounced so that distal lobe has forklike appearance; positioned near outer edge distally. Penial duct straight, positioned very close to outer edge.

**Type locality:** Flag Springs, White River Valley, Nye County, Nevada, T. 7 N, R. 62 E, NE ¼ section 33. Holotype, USNM 874664 (Figure 17H), collected by R. Hershler and P. Hovingh, 28 June 1992; paratypes, USNM 860691. The type locality, the northernmost spring of the Flag Spring complex, is a large rheocene (Figure 4A). Snails were collected on hard substrate in the pool just below the spring source.

**Remarks:** This species is compared with *P. hubbsi* above. The distribution of *P. sathos* is shown in Figure 49.

**Material examined:** NEVADA. *Nye County:* Flag Springs (north) (Figure 4A), USNM 860691, USNM 873165, USNM 874664, USNM 883856.—Flag Springs (middle), White River Valley, T. 7 N, R. 62 E, NW ¼ section 33, USNM 873179. *Lincoln County:* Camp Spring, White River Valley, T. 6 N, R. 60 E, NW ¼ section 36, USNM 874380, USNM 874663. *White Pine County:* Spring, Lund, White River Valley, T. 11 N, R. 62 E, NE ¼ section 4, USNM 874019, USNM 883591, USNM 883852.—Arnoldson Spring, White River Valley, T. 12 N, R. 61 E, SE ¼ section 12, USNM 874687.—Preston Big Spring, White River Valley, T. 12 N, R. 61 E, NE ¼ section 2, USNM 873198, USNM 874022, USNM 874673.

*Pyrgulopsis breviloba* Hershler, sp. nov.

Flag pyrg

(Figures 6G, 11C, 14D–F, 17L, M, 28D–F)

**Etymology:** From *brevis* (Latin), short, and *lobus*, projection; referring to the short penial lobe characterizing this species.

**Diagnosis:** Small, with low-trochoid shell. Penis large; filament medium length, distally bifid; lobe very short. Penial ornament a very small terminal gland.

**Description:** Shell (Figures 6G, 17L, M) low-trochoid,

apex usually eroded; width/height, 77–105%; height, 1.2–2.2 mm; width, 1.0–2.0 mm; whorls 2.75–3.75. Protoconch (Figure 11C) 1.25 whorls, diameter 0.29 mm, weakly wrinkled along inner edge near apex (sculpture sometimes coalescing to form weak spiral elements), otherwise smooth. Teleoconch whorls medium convexity; strongly shouldered, sometimes strongly angulate near aperture. Aperture crescent-shaped, usually disjunct. Inner lip usually thick, having medium width columellar shelf. Outer lip slightly thickened, strongly prosocline, without sinuation. Umbilicus rimate or perforate; umbilical region sometimes well excavated with adaxial ridge. Periostracum light brown, thick.

Operculum narrowly ovate, amber, darker in nuclear region; nucleus eccentric; dorsal surface smooth or weakly frilled near inner edge; outer margin sometimes having weak rim. Attachment scar narrowly thickened between nucleus and inner edge.

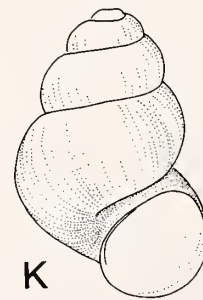
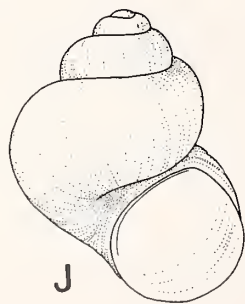
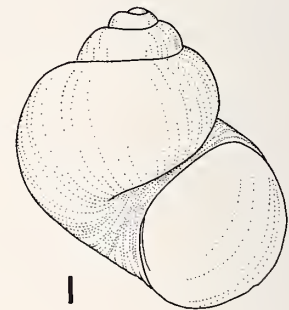
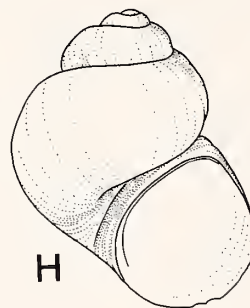
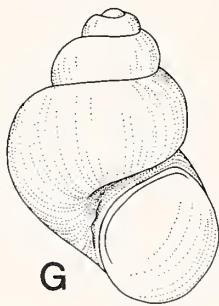
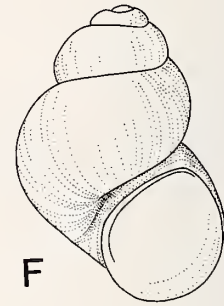
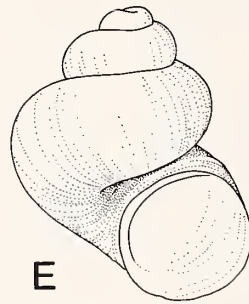
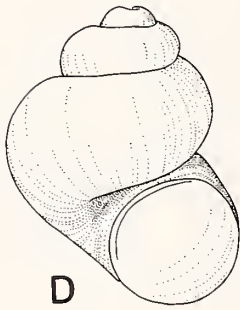
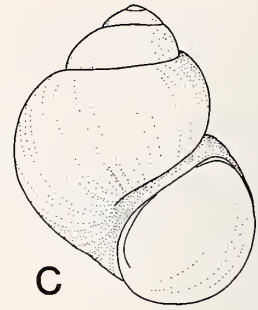
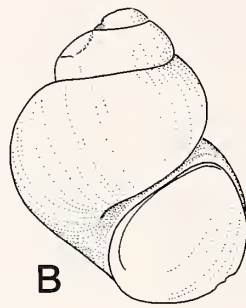
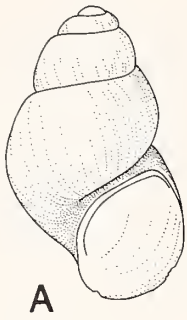
Radula (Figure 14D–F) 667 × 110 μm, with 67 rows of teeth. Central tooth 21 μm wide, with highly indented dorsal edge; lateral cusps, 5–6, sometimes partly fused dorsally; central cusp broad, spoonlike; basal cusps small, sometimes flanked on inner side by weakly developed second cusp. Basal tongue broad V-shaped, slightly longer than lateral margins, basal sockets medium depth. Lateral tooth formula 3-1-4; neck weakly flexed; outer wing 370% of cutting edge length. Inner marginal teeth with 33–34 cusps; cutting edge 33% of length of tooth. Outer marginal teeth with 29–32 cusps; cutting edge 27% of length of tooth. Stomach and style sac equal in length; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles medium to dark brown. Snout dark brown. Foot medium to dark brown, pigment usually heavier along anterior edge. Opercular lobe dark along inner edge, sometimes all around. Neck nearly unpigmented to dark. Pallial roof, visceral coil uniformly dark brown-black. Distal half of penis densely pigmented with internal grey granules.

Ctenidial filaments, 17, pleated; ctenidium abutting or slightly overlapping pericardium posteriorly. Osphradium small, narrow-ovate, centrally positioned. Renal gland longitudinal-oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Figure 21

Shells of *Pyrgulopsis* species. A. *P. militaris*, holotype, USNM 873203 (shell height, 1.4 mm). B. *P. militaris*, USNM 883921 (1.6 mm). C. *P. umbilicata*, holotype, USNM 873208 (2.0 mm). D. *P. umbilicata*, USNM 873202 (2.0 mm). E. *P. limaria*, holotype, USNM 873232 (1.7 mm). F. *P. limaria*, USNM 874291 (2.0 mm). G. *P. notidicola*, holotype, USNM 873215 (2.0 mm). H. *P. notidicola*, USNM 874286 (1.7 mm). I. *P. vinyardi*, holotype, USNM 874740 (2.0 mm). J. *P. imperialis*, holotype, USNM 874207 (1.8 mm). K. *P. imperialis*, USNM 874211 (1.6 mm). L. *P. sadai*, holotype, USNM 874397 (2.5 mm). M. *P. sadai*, USNM 883900 (2.9 mm). N. *P. sadai*, USNM 883851 (3.0 mm).





Ovary a little more than 1.0 whorl, filling most of digestive gland behind stomach, overlapping posterior and part of anterior chambers anteriorly. Distal female genitalia shown in Figure 28D. Albumen gland having small-medium (16–30%) pallial component. Capsule gland slightly shorter and narrower than albumen gland, sub-circular in section, rectal furrow pronounced. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a broad circular loop preceded by a proximal twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, narrow or clublike, longitudinal, extending to edge of albumen gland. Bursal duct originating from anterior edge at mid-line, abutting oviduct; up to 50% length of bursa, medium width. Seminal receptacle small, narrow, overlapping anterior bursa along ventral edge, well anterior to edge of albumen gland.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly and abutting edge of prostate gland. Prostate broadly ovate, pallial portion medium, narrowly ovate in section. Proximal pallial vas deferens having sharp bend. Penis (Figure 28E, F) large; elongate-rectangular, base weakly folded along inner edge; filament medium length, rectangular, as wide as base, distally bifid; lobe extremely short, tapered, longitudinal. Terminal gland very small, circular, borne on ventral surface of lobe. Penial duct straight, near outer edge.

**Type locality:** Flag Springs, White River Valley, Nye County, Nevada, T. 7 N, R. 62 E, NE ¼ section 32. Holotype, USNM 873174 (Figure 17L), collected by J. J. Landye, 1 September 1973; paratypes, USNM 860689. Flag Springs comprises three springs draining to Sunnyside Creek, located within the Wayne Kirch Wildlife Management Area. The type locality, the middle of the three, nearly north-south trending springs; is a narrow rheocene having a relatively large discharge.

**Remarks:** This snail and two other species from White River Valley, *P. lata* and *P. gracilis* (described next), share unusual features of strongly shouldered shell whorls, angular aperture, and well-developed columellar shelf. These species, which occur in closely adjacent

spring complexes, are also closely similar in shape of central and lateral radular teeth, and configuration of distal female genitalia, but their penes are dissimilar, and that of *P. breviloba* is unique in its combination of elongate shape; very small lobe bearing weak terminal gland; and broadly rectangular, distally bifurcate filament. *Pyrgulopsis bifurcata* (described below), from Carico Lake Basin, also has a bifurcate penial filament, but has a completely different pattern of penial ornament than *P. breviloba* and also differs in various other features. The distribution of *P. breviloba* is shown in Figure 50.

**Material examined:** NEVADA. *Lincoln County:* Meloy Spring, Dry Lake Valley, T. 5 N, R. 65 E, NE ¼ section 32, USNM 874671. *Nye County:* Flag Springs (middle), USNM 860689, USNM 873174, USNM 883846.—Flag Springs (north), T. 7 N, R. 62 E, NE ¼ section 30, USNM 873188, USNM 874029, USNM 874031, USNM 883874.

*Pyrgulopsis lata* Hershler, sp. nov.

Butterfield pyrg

(Figures 6H, 12D, 18A, 29A–E)

**Etymology:** From *latus* (Latin), broad or wide; referring to the prominent columellar shelf characterizing shells of this species.

**Diagnosis:** Small, with ovate to narrow-conic shell. Penis large, filament short, lobe short. Penial ornament a small, fragmented terminal gland; very small Dg1, and small ventral gland.

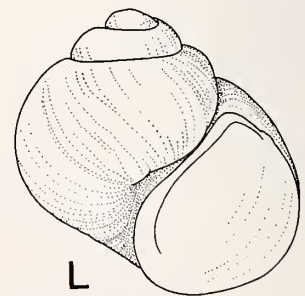
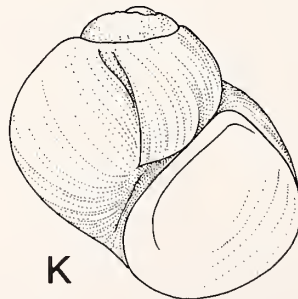
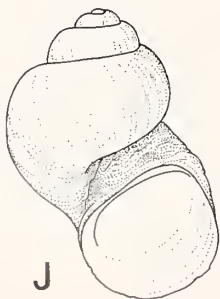
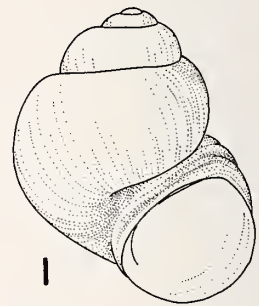
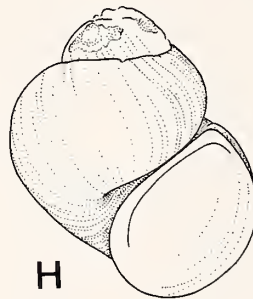
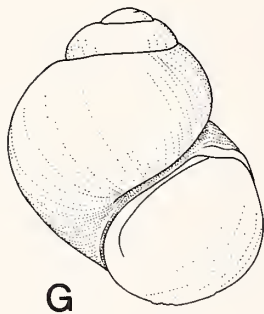
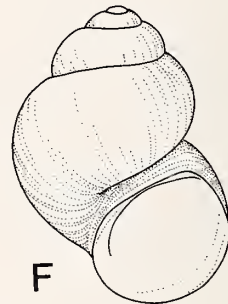
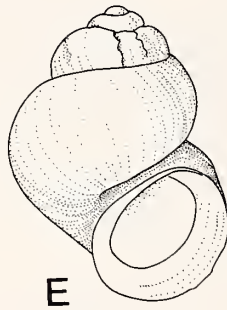
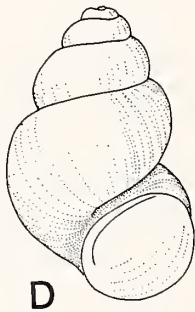
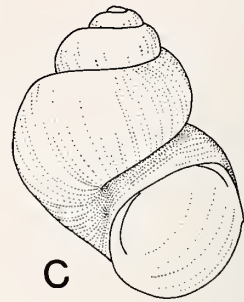
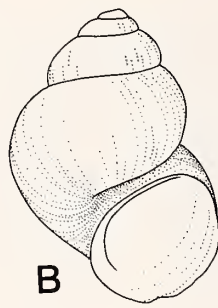
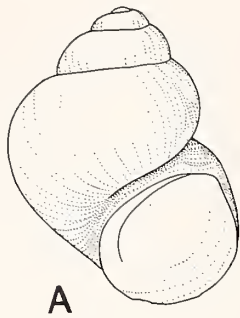
**Description:** Shell (Figures 6H, 18A) ovate- to narrow-conic, apex usually eroded, width/height, 66–84%; height, 1.6–2.1 mm; width, 1.2–1.6 mm; whorls, 3.75–4.25. Protoconch 1.25 whorls, diameter 0.28 mm, early portion wrinkled along inner edge, otherwise smooth. Teleoconch whorls moderately convex, strongly shouldered; adapical region strongly angulate or keel-like; body whorl often slightly disjunct behind the aperture. Aperture ovate, angled above, usually disjunct, sometimes broadly so. Inner lip slightly thickened, having broad, well-developed columellar shelf. Outer lip slightly thickened, prosocline, without sinuation. Umbilicus perforate to broadly open. Periostracum light brown.

Operculum (Figure 12D) ovate, light amber, inner edge

←

Figure 22

Shells of *Pyrgulopsis* species. A. *P. augustae*, holotype, USNM 874402 (shell height, 2.3 mm). B. *P. pictilis*, holotype, USNM 874401 (2.6 mm). C. *P. pictilis*, USNM 860713 (2.4 mm). D. *P. basiglans*, holotype, USNM 874280 (1.5 mm). E. *P. bifurcata*, holotype, USNM 874306 (1.3 mm). F. *P. pellita*, holotype, USNM 883850 (3.2 mm). G. *P. leporina*, holotype, USNM 874336 (2.9 mm). H. *P. humboldtensis*, holotype, USNM 874722 (2.2 mm). I. *P. humboldtensis*, USNM 874725 (2.5 mm). J. *P. humboldtensis*, USNM 874719 (2.5 mm). K. *P. hamlinensis*, holotype, USNM 883215 (2.0 mm).



straight, nucleus eccentric; dorsal surface smooth. Attachment scar slightly thickened between nucleus and inner edge.

Radula  $575 \times 85 \mu\text{m}$ , with 74 rows of teeth. Central tooth  $17 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 6–7 (often fused dorsally), central cusp medium width to broad, spoonlike; basal cusps medium-sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula, 3(4)-1-5; neck weakly flexed; outer wing 257% of cutting edge length. Inner marginal teeth with 34–36 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 31–34 cusps; cutting edge occupying 24% of length of tooth. Stomach longer than style sac, anterior chamber larger than posterior chamber; stomach caecum very small to nearly absent.

Cephalic tentacles light to dark grey-brown, sometimes lighter around eyespots and along narrow central zone. Snout medium to dark grey-brown. Foot, neck light to dark grey-brown. Opercular lobe dark along inner edge and sides, light-dark elsewhere. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally for most of length.

Ctenidial filaments, 15, weakly pleated; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, narrow, positioned centrally. Renal gland slightly oblique; kidney opening white. Rectum broadly overlapping genital ducts.

Ovary 1.0–1.25 whorls, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 29A. Albumen gland having short pallial component. Capsule gland slightly shorter and narrower than albumen gland, sub-circular in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a short, terminal slit often mounted on small raised swelling or papilla; anterior extension short. Coiled oviduct a circular loop usually preceded by small anterior twist or bend. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix considerably narrower and shorter than albumen gland, ovate, longitudinal or slightly oblique, less than 33% of length posterior to gland. Bursal duct originating from anterior edge near mid-line, medium length and width, slightly broader distally. Seminal receptacle small, pouchlike, overlapping or abutting ven-

tral edge of anterior portion of bursa (a little dorsal to ventral edge of albumen gland).

Testis 1.0–1.25 whorls, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber anteriorly. Prostate gland bean-shaped, pallial portion short, narrow ovate in section. Proximal pallial vas deferens with undulation. Penis (Figure 29B-E) large, base rectangular, often elongate and expanded distally, weakly folded along inner edge; filament short, medium width, tapering to pointed tip, longitudinal or slightly oblique; lobe short to near absent, hemispherical, slightly oblique. Terminal gland small, usually divided into two to six small dotlike units along edge of lobe. Dg1 very small, rarely including a second, dotlike unit, borne on low swelling, near outer edge just proximal to filament. Ventral gland small, narrow, borne on low swelling, often curved into U-shape and extending near or onto edge of lobe, positioned near outer edge distally. Penial duct straight, near outer edge.

**Type locality:** Butterfield Springs, White River Valley, Nye County, Nevada, T. 7 N, R. 62 E, NE  $\frac{1}{4}$  section 28 (Figure 50). Holotype, USNM 874667 (Figure 18A), collected by R. Hershler and P. Hovingh, 28 June 1992; paratypes, USNM 860697. The type locality is a small rheocrene.

**Remarks:** *Pyrgulopsis lata* differs from similarly shelled White River Valley species (see above) in having a very weak penial lobe; small, distal Dg1 (absent in the above); and large ventral gland (smaller in *P. breviloba*, absent in *P. gracilis*). *Pyrgulopsis lata* resembles *P. saxatilis* (described below), from western Bonneville Basin, in penial form and ornament, but is readily distinguished by its narrower shell, fragmented terminal gland, larger bursa copulatrix with shorter duct, and more posteriorly positioned seminal receptacle.

**Material examined:** NEVADA. *Nye County:* Butterfield Springs, USNM 860697, USNM 873167, USNM 874667.

*Pyrgulopsis gracilis* Hershler, sp. nov.

Emigrant pyrg

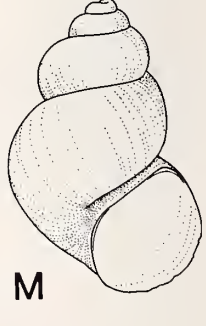
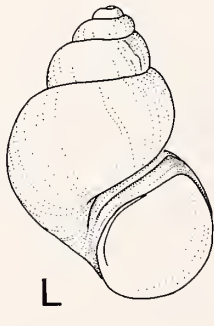
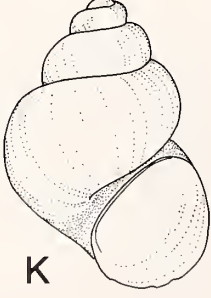
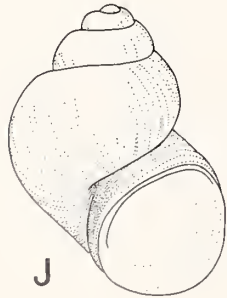
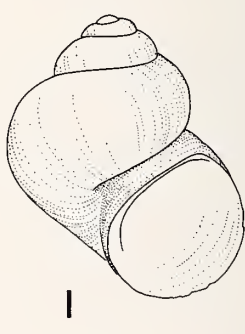
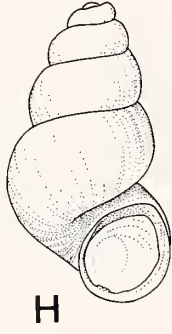
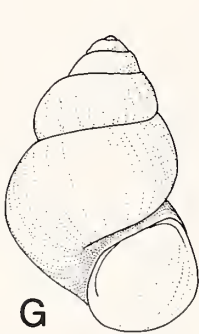
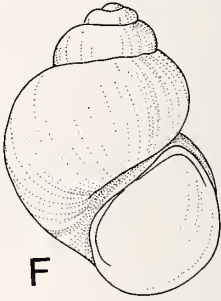
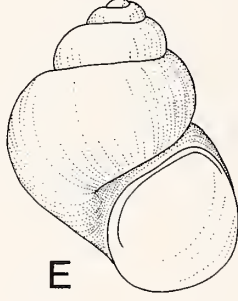
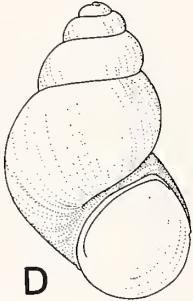
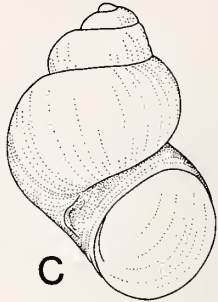
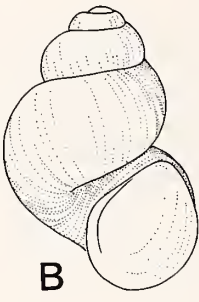
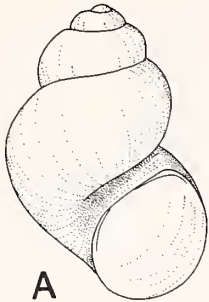
(Figures 6I, 11D, 18B, C, 29F–H)

**Etymology:** From *gracilis* (Latin), slender; referring to the narrow penial filament characterizing this species.

←

Figure 23

Shells of *Pyrgulopsis* species. A. *P. peculiaris*, holotype, USNM 883933 (shell height, 2.2 mm). B. *P. peculiaris*, USNM 883622 (2.8 mm). C. *P. peculiaris*, USNM 883603 (2.5 mm). D. *P. peculiaris*, USNM 874683 (2.5 mm). E. *P. peculiaris*, USNM 874319 (2.5 mm). F. *P. peculiaris*, USNM 883227 (2.2 mm). G. *P. peculiaris*, USNM 883222 (1.9 mm). H. *P. anguina*, holotype, USNM 874678 (2.3 mm). I, J. *P. anguina*, USNM 883205 (2.7 mm, 2.6 mm, respectively). K. *P. saxatilis*, holotype, USNM 883237 (1.3 mm). L. *P. saxatilis*, USNM 860726 (1.1 mm).



**Diagnosis:** Small, with broad- to narrow-conic shell. Penis medium-sized, filament long, lobe short or absent. Penial ornament a small terminal gland and large penial gland.

**Description:** Shell (Figures 6I, 18B, C) narrow conic, but apex usually highly eroded, producing a broadly conical shape; width/height, 81–92%; height, 1.6–1.9 mm; width, 1.3–1.6 mm; up to 4.0 whorls remaining. Protoconch (Figure 11D) 1.25 whorls, diameter 0.28 mm, initial 0.75 whorl finely wrinkled, later portion near smooth. Teleoconch whorls moderately convex, shoulders well developed, often forming a pronounced subsutural angulation on penultimate two whorls. Aperture ovate, well angled above, broadly adnate to slightly disjunct. Inner lip thick, with narrow columellar shelf. Outer lip thin-thick, prosocline, weakly sinuate. Umbilicus absent or rimate. Periostracum tan, brown, or reddish.

Operculum ovate, amber, darker in nuclear region; nucleus eccentric; dorsal surface smooth. Attachment scar margin slightly thickened between nucleus and inner edge, and along inner edge.

Radula  $490 \times 80 \mu\text{m}$ , with 60 rows of teeth. Central tooth  $18 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 5–6; central cusp medium width, spoonlike; basal cusps medium-sized. Basal process V-shaped, slightly longer than lateral margins, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 30–31 cusps; cutting edge occupying 35% of length of tooth. Outer marginal teeth with 27–31 cusps; cutting edge occupying 28% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles light to medium brown, often unpigmented around eyespots and along narrow central region. Snout medium to dark brown. Foot light to dark brown-black, especially dark along anterior edge. Opercular lobe usually medium brown, often slightly darker along sides. Neck nearly unpigmented to medium brown, often much lighter than rest of head. Pallial roof, visceral coil near uniform dark brown-black. Penial filament darkly pigmented internally.

Ctenidial filaments 19, weakly pleated; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of cte-

nidium. Renal gland oblique, sometimes strongly so; kidney opening grey-white. Rectum broadly overlapping pallial oviduct and slightly overlapping prostate gland.

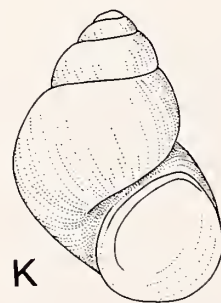
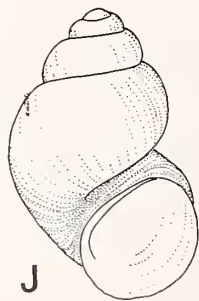
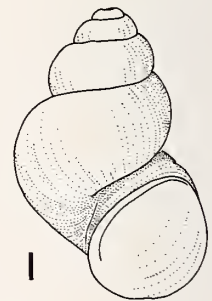
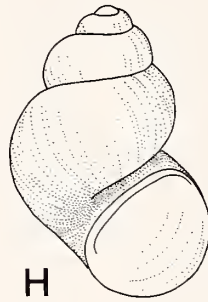
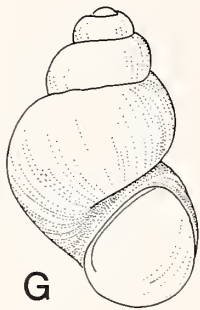
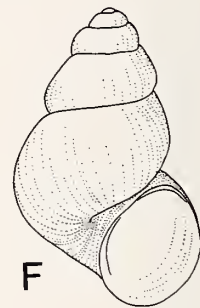
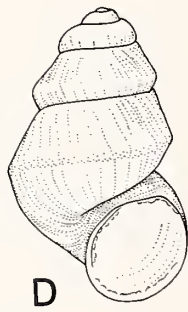
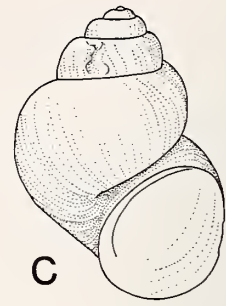
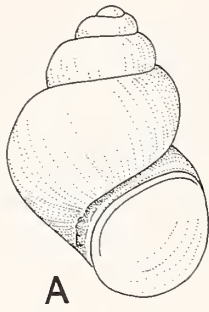
Ovary 0.75 whorl, filling 50% of digestive gland behind stomach, partly overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 29F. Albumen gland having short pallial component. Capsule gland slightly shorter and narrower than albumen gland, ovate in section; rectal furrow weak or absent. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a short terminal slit without anterior extension. Coiled oviduct a tight sub-circular coil preceded by weak posterior bend. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge near mid-line, slightly shorter to slightly longer than bursa, medium width. Seminal receptacle short, narrow, overlapping or abutting proximal bursal duct, sometimes slightly overlapped by albumen gland.

Testis 1.25 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland bean-shaped, pallial section short, ovate in section. Proximal pallial vas deferens having weak undulation, almost straight. Penis (Figure 29G, H) medium-sized; base rectangular, folded along inner edge; filament as long as base, narrow, gently tapering, longitudinal; lobe short to almost absent, knoblike, longitudinal. Terminal gland small, sometimes very reduced, circular, sometimes divided into two to three dotlike units, usually ventral. Penial gland filling 50% of filament length, narrow, centrally positioned, usually bulging below inner edge of filament. Filament also sometimes bearing small, dotlike gland near base. Penial duct straight, near outer edge.

**Type locality:** Emigrant Springs, White River Valley, Nye County, Nevada, T. 9 N, R. 62 E, NE  $\frac{1}{4}$  section 19 (Figure 50). Holotype, USNM 873158 (Figure 18B), collected by J. J. Landye, 2 September 1973; paratypes, USNM 860698. Emigrant Springs comprises a spring complex alongside Nevada State HWY 318. The type locality, the northernmost spring in this complex, is a small rheocrene.

Figure 24

Shells of *Pyrgulopsis* species. A. *P. variegata*, holotype, USNM 883627 (shell height, 2.7 mm). B. *P. variegata*, USNM 883888 (2.5 mm). C. *P. variegata*, USNM 874713 (2.7 mm). D. *P. variegata*, USNM 883599 (3.1 mm). E. *P. hovinghi*, holotype, USNM 874075 (2.5 mm). F. *P. millenaria*, holotype, USNM 874720 (2.5 mm). G. *P. lentiglans*, holotype, USNM 874724 (1.8 mm). H. *P. lentiglans*, USNM 854540 (2.2 mm). I. *P. plicata*, holotype, USNM 883594 (2.5 mm). J. *P. plicata*, USNM 860727 (2.7 mm). K. *P. fusca*, holotype, USNM 883439 (2.7 mm). L. *P. fusca*, USNM 883573 (3.3 mm). M. *P. fusca*, USNM 883442 (2.9 mm).



**Remarks:** This species has an unique penial morphology featuring a very slender filament with an elongate penial gland along its inner edge. Although *P. gracilis* otherwise resembles two other species found in White River Valley (see above), this snail is further distinguished by stronger protoconch microsculpture, unfused cusps on the central radular teeth, and the more posteriorly positioned bursa copulatrix.

**Material examined:** NEVADA. *Nye County*: Emigrant Springs (north), USNM 860698, USNM 873158, USNM 874382, USNM 883842.—Emigrant Springs (south), White River Valley (Figure 4B), T. 9 N, R. 62 E, NE ¼ section 30, USNM 883885.

*Pyrgulopsis marcida* Hershler, sp. nov.

Hardy pyrg

(Figures 6J, 18D–F, 30A–C)

**Etymology:** From *marcidus* (Latin), withered or wasted; referring to the reduced penial glands of this species.

**Diagnosis:** Small to medium-sized, with ovate- to elongate-conic shell. Penis medium-large; filament and lobe medium length. Penial ornament a small terminal gland, very small penial gland (sometimes absent), and occasional small gland on ventral surface of lobe.

**Description:** Shell (Figures 6J, 18D–F) ovate- to elongate conic, width/height, 66–86%; height, 1.6–3.9 mm; width, 1.2–3.0 mm; whorls, 3.5–4.75. Protoconch 1.25 whorls, diameter 0.35 mm, smooth. Teleoconch whorls moderately convex, shouldered, often having deep sutures; body whorl often slightly disjunct behind the aperture. Aperture ovate, narrowly adnate to slightly disjunct. Inner lip thin, without columellar shelf. Outer lip usually thin, orthocone or slightly prosocline, without situation. Umbilicus narrow-perforate. Periostracum tan.

Operculum ovate, amber, reddish in nuclear region; nucleus eccentric; dorsal surface frilled; outer margin having weak rim. Attachment scar thick (especially so along inner edge) all around.

Radula  $687 \times 119 \mu\text{m}$ , with 57 rows of teeth. Central tooth  $28 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 7–8; central cusp medium width, rounded; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4-1-5; neck well

flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 31–34 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 37–39 cusps; cutting edge occupying 24% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum medium-sized.

Cephalic tentacles very light grey-brown. Snout light to medium grey. Foot light to medium grey, darkest along anterior edge. Opercular lobe medium grey to black along anterior edge and sides, sometimes all around (central region lighter). Neck light to medium grey-brown. Pallial roof and visceral coil uniformly dark brown-black. Penial filament darkly pigmented internally.

Ctenidial filaments, 21, pleated; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, abutting or slightly overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 30A. Albumen gland having short pallial component. Capsule gland as wide and slightly shorter to as long as albumen gland, sub-circular in section; rectal furrow deep. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two short, overlapping tight coils, usually posterior-oblique in orientation. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix medium length and width, ovate, usually longitudinal, with 33% or less of length posterior to gland. Bursal duct originating from anterior edge near mid-line, shorter than bursa, medium width. Seminal receptacle small, pouchlike, overlapping proximal bursal duct near ventral edge of albumen gland, often shallowly embedded in gland.

Testis 1.75–2.0 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and small portion of anterior stomach chambers. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having sharp, reflexed bend. Penis (Figure 30B, C) medium-large; base rectangular, sometimes weakly folded along inner edge; filament slightly shorter than base, medium width, tapering to point, near longitudinal to strongly oblique; lobe short,

←

Figure 25

Shells of *Pyrgulopsis* species. A. *P. chamberlini*, holotype, USNM 883576 (2.8 mm). B, C. *P. chamberlini*, USNM 883944 (2.9 mm, 3.8 mm, respectively). D. *P. inopinata*, holotype, USNM 883943 (2.9 mm). E, F. *P. inopinata*, USNM 860730 (2.9 mm, 2.8 mm, respectively). G. *P. nonaria*, holotype, USNM 883566 (2.5 mm). H. *P. transversa*, holotype, USNM 883221 (2.3 mm). I. *P. transversa*, USNM 860732 (2.3 mm). J. *P. transversa*, USNM 883422 (2.4 mm). K. *P. transversa*, USNM 883597 (3.0 mm).

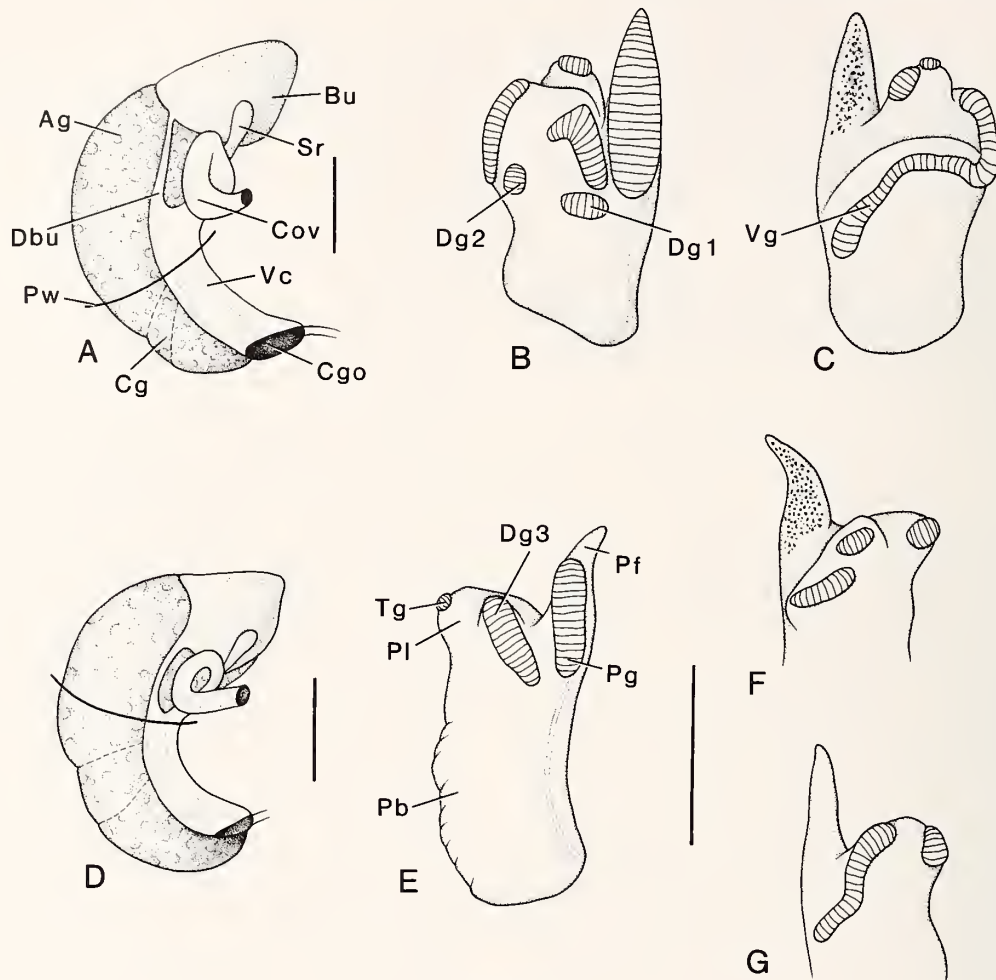


Figure 26

Genitalia of *Pyrgulopsis* species. (A–C, *P. fausta*, USNM 873175; D–G, *P. deaconi*, USNM 873355). A. Female glandular oviduct and associated structures, bar = 0.25 mm. B. Dorsal aspect of penis, scale as in A. C. Ventral aspect of penis, scale as in A. D. Female glandular oviduct and associated structures, bar = 0.25 mm. E. Dorsal aspect of penis, bar = 0.5 mm. F, G, Ventral aspect of distal penis, scale as in E. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cgo = opening of capsule gland, Cov = coiled oviduct, Dbu = duct from bursa copulatrix, Dg1 = proximal dorsal gland on penis, Dg2 = dorsal gland near inner, distal edge of penis, Dg3 = dorsal gland near outer edge of penial lobe, Pb = base of penis, Pf = penial filament, Pg = gland on penial filament, Pl = lobe of penis, Pw = pallial wall, Sr = seminal receptacle, Vc = ventral channel of capsule gland, Vg = gland on ventral surface of penis.

sometimes near absent, knoblike, near longitudinal to oblique. Terminal gland small, narrow, variably oriented or reduced to two to three dotlike units, usually ventral. Penial gland very small, ovate, positioned near base of filament, often absent. Dotlike Dg2 rarely present along inner edge distally. Ventral lobe sometimes bearing small, often slightly raised gland proximally (adjacent to terminal gland) that may represent a reduced ventral gland. Penial duct straight, near outer edge.

**Type locality:** Hardy Springs, White River Valley, Nye County, Nevada, T. 9 N, R. 61 E, SW  $\frac{1}{4}$  section 13. Ho-

lotype, USNM 873154 (Figure 18D), collected by J. J. Landye, 3 September 1973; paratypes, USNM 860711. The type locality is a small rheocrene.

**Remarks:** This species resembles *P. anatina* (described below), from Duckwater Valley, but differs in having a reflexed pallial vas deferens, squatter penis with shorter, broader lobe and filament; occasional presence of gland on ventral penis, smaller penial gland, narrower oviduct coil with two well-developed loops, and smaller seminal receptacle. Snails from Cave Valley have considerably lighter



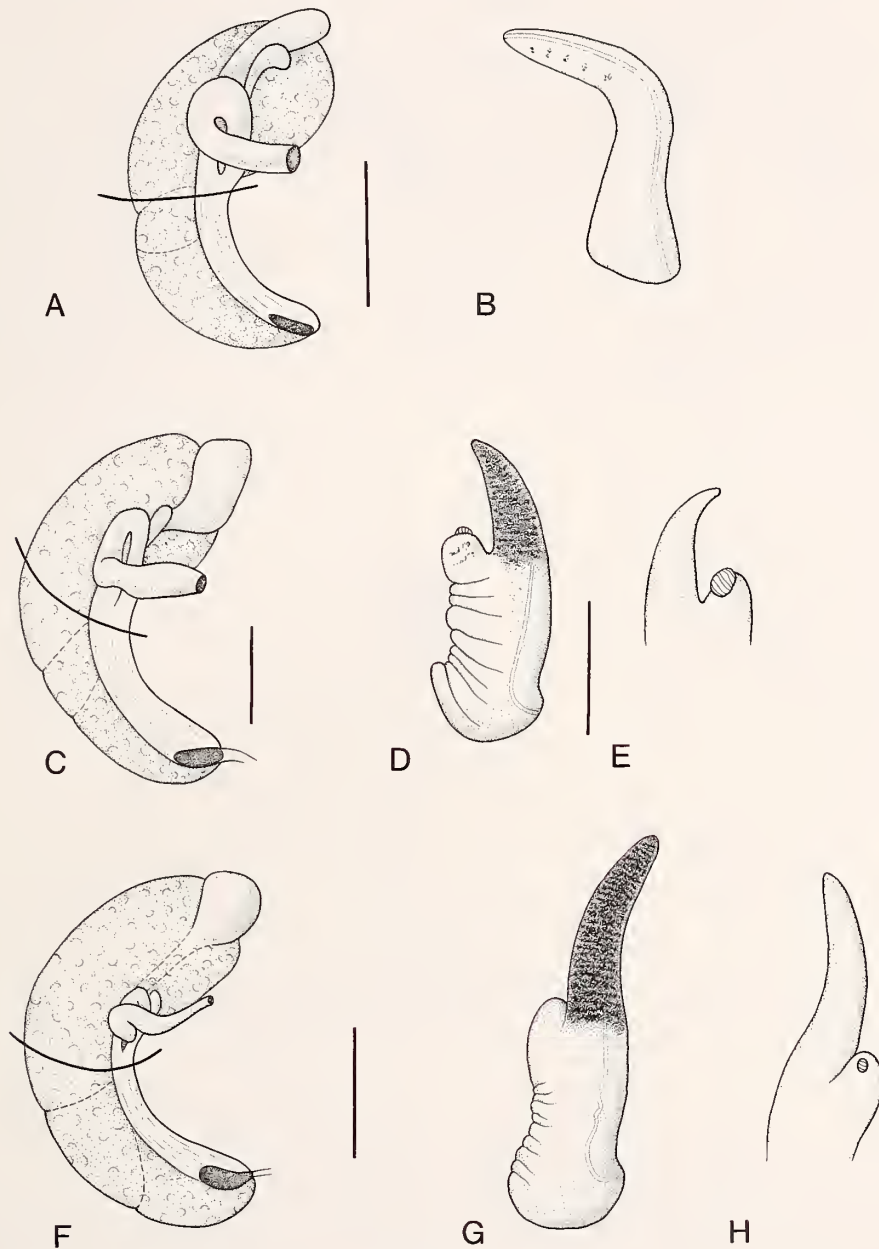


Figure 27

Genitalia of *Pyrgulopsis* species (A, B, *P. coloradensis*, USNM 873360, bar = 0.25 mm; C–E, *P. montana*, USNM 860694; F–H, *P. hubbsi*, USNM 873166). A. Female glandular oviduct and associated structures, bar = 0.25 mm. B. Dorsal aspect of penis, scale as in A. C. Female glandular oviduct and associated structures, bar = 0.25 mm. D. Dorsal aspect of penis, bar = 0.25 mm. E. Ventral aspect of distal penis, scale as in D. F. Female glandular oviduct and associated structures, bar = 0.5 mm. G. Dorsal aspect of penis, scale as in F. H. Ventral aspect of distal penis, scale as in G.

body pigmentation that those from White River Valley. The distribution of this snail is shown in Figure 50.

**Material examined:** NEVADA. *Nye County*: Hardy Springs, USNM 860711, USNM 873154, USNM 874373, USNM 874662.—Emigrant Springs (south), White River

Valley (Figure 4B), T. 9 N, R. 62 E, NE ¼ section 30, USNM 874688.—Emigrant Springs (north), White River Valley, T. 9 N, R. 62 E, NE ¼ section 19, USNM 873170, USNM 883843.—Butterfield Springs, White River Valley, T. 7 N, R. 62 E, NE ¼ section 28, USNM 874378, USNM

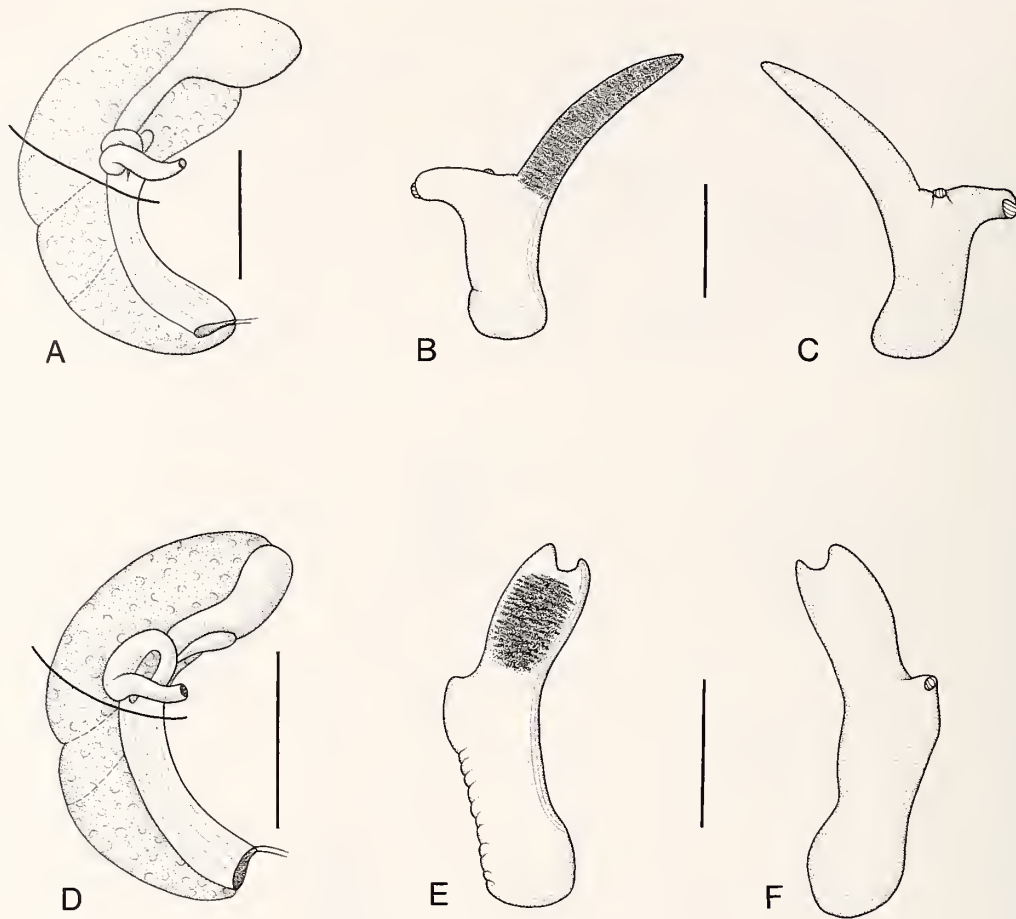


Figure 28

Genitalia of *Pyrgulopsis* species (A–C, *P. sathos*, USNM 860691; D–F, *P. breviloba*, USNM 860689). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of penis.

883972, USNM 883973. *Lincoln County*: Silver Springs, White River Valley, T. 8 N, R. 62 E, SW  $\frac{1}{4}$  section 14, USNM 874672.—Springs, Parker Station, Cave Valley, T. 9 N, R. 64 E, NW  $\frac{1}{4}$  section 6, USNM 874682. *White Pine County*: Ruppess Boghole, White River Valley, T. 10 N, R. 62 E, SE  $\frac{1}{4}$  section 7, USNM 874685.

#### Species from Isolated Basins in Nevada

*Pyrgulopsis turbatrix* Hershler, sp. nov.

Southeast Nevada pyrg

(Figures 6K, 18G–J, 30D–F)

*Pyrgulopsis micrococcus* (Pilsbry, 1893), Hershler, 1989: 183 [not Pilsbry, 1893; in part; Frenchman Flat].—Hershler & Pratt, 1990:285, 286 [in part; northern Spring Mountains].

**Etymology:** *Turbatrix* (Latin), disturber, trouble-maker;

referring to the difficulty encountered in separating this species from *P. micrococcus*.

**Diagnosis:** Medium-sized, with narrow-conic to turriiform shell. Penis large; filament medium length, lobe medium length. Penial ornament a small terminal gland, and very small penial gland (sometimes absent).

**Description:** Shell (Figures 6K, 18G–J) narrow-conic to turriiform, width/height, 56–76%; height, 2.1–3.6 mm; width, 1.5–2.2 mm; whorls, 4.25–5.5. Protoconch 1.4–1.5 whorls, diameter 0.36 mm; surface smooth except for very weak wrinkling at apex. Teleoconch whorls medium to highly convex, shoulders absent to well developed (often having weak sub-sutural angulation); body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thin or slightly thickened, columellar shelf absent or narrow. Outer lip thin, orthocline or slightly prosocline,

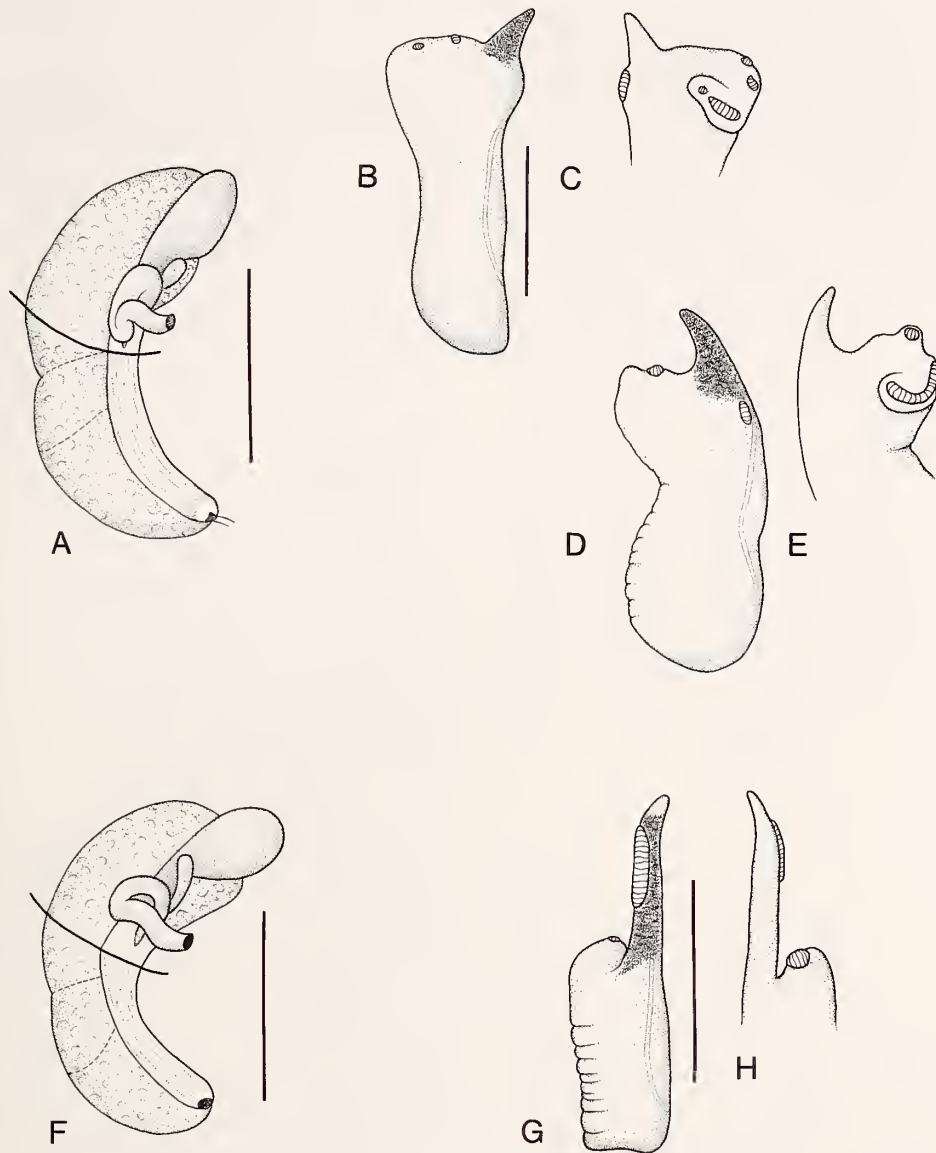


Figure 29

Genitalia of *Pyrgulopsis* species (A, D, E, *P. lata*, USNM 873167; B, C, *P. lata*, USNM 860697; F–H, *P. gracilis*, USNM 860698). A. Female glandular oviduct and associated structures, bar = 0.5 mm. B. Dorsal aspect of penis, bar = 0.5 mm. C. Ventral aspect of distal penis, scale as in B. D. Dorsal aspect of penis, scale as in B. E. Ventral aspect of distal penis, scale as in B. F. Female glandular oviduct and associated structures, bar = 0.5 mm. G. Dorsal aspect of penis, bar = 0.5 mm. H. Ventral aspect of distal penis, scale as in G.

without sinuation. Umbilicus rimate or shallowly perforate. Periostracum tan-brown.

Operculum ovate, amber, nuclear region slightly darker; nucleus eccentric; dorsal surface weakly frilled; outer margin having weak rim. Attachment scar slightly thickened all around.

Radula  $650 \times 100 \mu\text{m}$ , with 60 rows of teeth. Central tooth  $25 \mu\text{m}$  wide, with medium to highly indented dorsal edge; lateral cusps, 5–6; central cusp narrow, daggerlike;

basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck medium flexed; outer wing 180% of cutting edge length. Inner marginal teeth with 19–22 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 26–29 cusps; cutting edge occupying 30% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

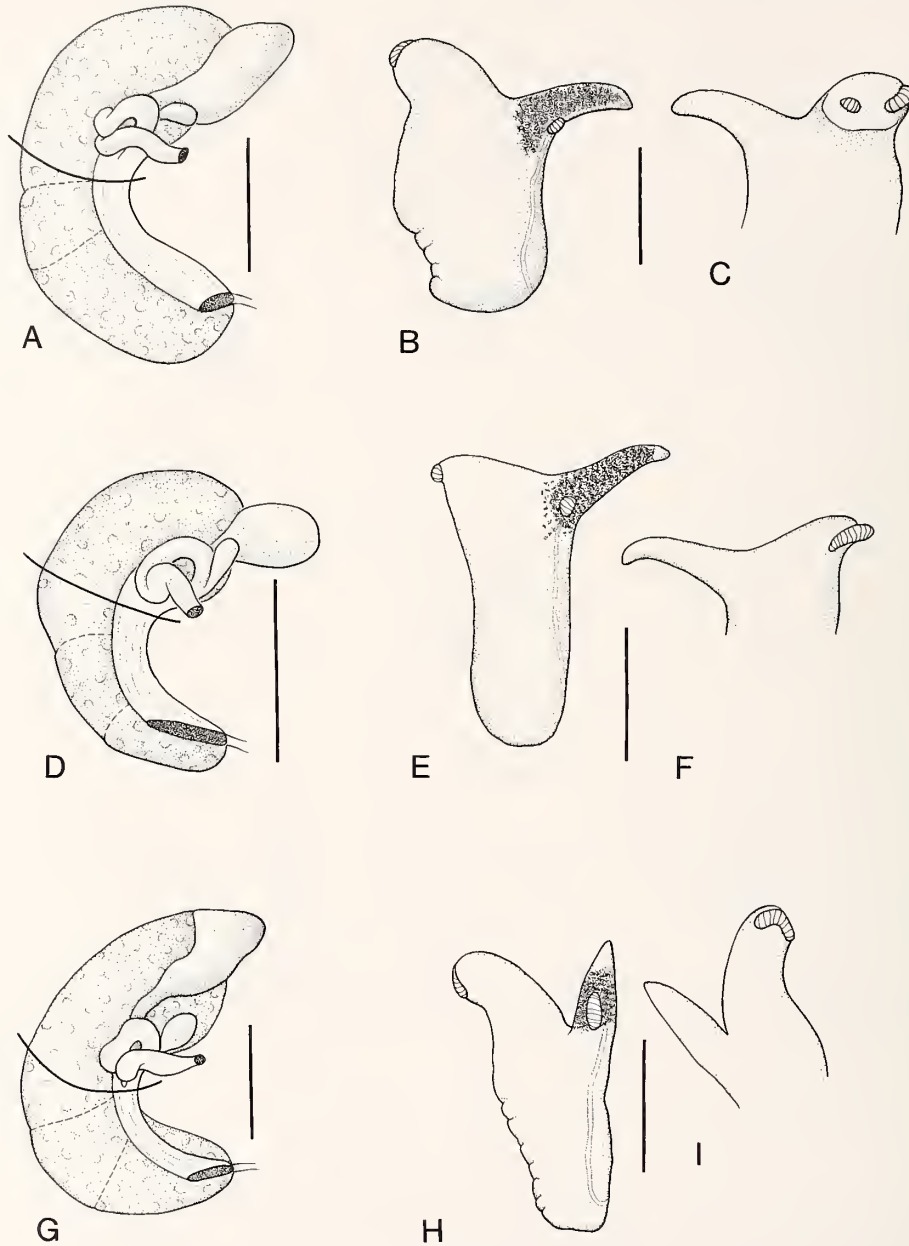


Figure 30

Genitalia of *Pyrgulopsis* species (A–C, *P. marcida*, USNM 874662; D–F, *P. turbatrrix*, USNM 860699; G–I, *P. sterilis*, USNM 860714). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis.

Cephalic tentacles pigmented proximally with subepithelial medium grey streak; sometimes having light to medium grey epithelial cover as well. Snout, foot light to medium grey. Opercular lobe dark along inner edge. Neck unpigmented except for scattered black granules to medium grey. Pallial roof, visceral coil black. Penial filament darkly pigmented, distal base often similarly pig-

mented; remaining dorsal penis having scattered black pigment granules.

Ctenidial filaments, 18, pleated; ctenidium abutting or slightly overlapping pericardium posteriorly. Osphradium small (20–25%), narrowly ovate, positioned centrally or slightly posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum

broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 30D. Albumen gland having medium pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture an elongate, terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop (sometimes kinked at mid-length) usually preceded by a short posterior-oblique twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, usually positioned along ventral edge of gland, 50–67% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, duct 50% of bursa length, medium width. Seminal receptacle medium-sized, pouchlike, positioned near ventral edge of albumen gland, overlapping anteriormost bursa.

Testis 2.0 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped (weakly curved), pallial portion short, ovate in section. Proximal pallial vas deferens straight, slightly undulating, or with weak bend. Penis (Figure 30E, F) large; base rectangular, weakly folded or smooth; filament medium length and width, tapering to point, oblique; lobe slightly shorter than filament, broadly triangular, slightly oblique. Terminal gland small, narrow (rarely ovate), usually longitudinal and ventral. Penial gland very small (often absent), considerably narrower than filament, positioned near base of filament. Penial duct straight, near outer edge.

**Type locality:** Horseshutem Springs, Pahrump Valley, Nye County, Nevada, T. 17 S, R. 53 E, SE ¼ section 27. Holotype, USNM 883978 (Figure 18G), collected by D. W. Sada, 20 July 1995; paratypes, USNM 860699. The type locality is a very small rheocrene highly impacted by cattle and water diversion (Figure 3A).

**Remarks:** This snail was previously confused with *P. micrococcus*, which also occurs in southeastern Nevada, but differs in its more elongate shell; narrower, usually longitudinal (not transverse) terminal gland on the penis; and frequent presence of a penial gland. *Pyrgulopsis turbatrix* also closely resembles *P. sterilis* (described below), which is found in isolated basins to the north, but differs in its broader penial lobe, smaller penial gland, and longitudinal orientation of terminal gland; and in having fewer cusps on the marginal radular teeth. *Pyrgulopsis turbatrix* occurs not only in several isolated basins in southwestern Nevada (Frenchman Flat, Indian Springs Valley, Pahrump Valley), but also in Colorado River drainage (Las Vegas Valley) and Death Valley system (Amargosa Flat) (Figure 50). Snails from Las Vegas Val-

ley do not have a penial gland, but otherwise conform to *P. turbatrix* in all features.

**Material examined:** NEVADA. *Clark County:* La Madre Spring, Red Rock Wash, Las Vegas Valley, T. 20 S, R. 58 E, NW ¼ section 6, USNM 874458, USNM 883981.—Stream, east of Willow Spring, Red Rock Wash, Las Vegas Valley, T. 21 S, R. 58 E, NW ¼ section 4, USNM 874009, USNM 874020, USNM 874214, USNM 874455, USNM 883656.—Willow Spring, Red Rock Wash, Las Vegas Valley, T. 20 S, R. 58 E, SE ¼ section 32, USNM 873186.—Lost Canyon Spring, Red Rock Wash, Las Vegas Valley, T. 21 S, R. 58 E, NE ¼ section 4, USNM 883977.—Willow Spring, Indian Springs Valley, T. 18 S, R. 55 E, NE ¼ section 2, USNM 874765, USNM 883551.—Willow Creek (just below Willow Spring), Indian Springs Valley, T. 18 S, R. 55 E, section 2, USNM 854065.—Cold Creek Spring, Indian Springs Valley, T. 18 S, R. 55 E, SE ¼ section 1, USNM 854738, USNM 873451, USNM 883550. *Nye County:* Horseshutem Springs (Figure 3A), USNM 860699, USNM 883978.—Grapevine Springs, Amargosa Flat, T. 17 S, R. 53 E, SW ¼ section 21, USNM 874756, USNM 883980.—Cane Spring, Frenchman Flat, T. 13 S, R. 52 E, NE ¼ section 26, USNM 857936, USNM 874775.

*Pyrgulopsis sterilis* Hershler, sp. nov.

Sterile basin pyrg

(Figures 6L, 18K, L, 30G–I)

**Etymology:** *Sterilis* (Latin), unfruitful or barren; referring to occurrence of this species in the fishless region of south-central Nevada referred to as the “area of sterile basins” by Hubbs & Miller (1948).

**Diagnosis:** Medium-sized to large, with ovate- to narrow-conic shell. Penis medium-sized, filament and lobe medium length. Penial ornament of small terminal and penial glands.

**Description:** Shell (Figures 6L, 18K, L) ovate- to narrow-conic, apex often eroded; width/height, 63–83%; height, 2.2–4.0 mm; width, 1.8–2.6 mm; whorls, 3.75–5.25. Protoconch 1.3 whorls, diameter 0.38 mm, initial 0.75 whorl wrinkled, later portion smooth or having a few very weak spiral striae. Teleoconch whorls highly convex, sometimes weakly loosened, producing scalariform appearance, shoulders weakly developed. Aperture ovate, narrowly adnate or slightly disjunct. Inner lip thick in larger specimens, without columellar shelf. Outer lip thin, orthocline-weakly prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum dark brown.

Operculum ovate, dark amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 970 × 160 μm, with 69 rows of teeth. Central

tooth 31  $\mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 5–6; central cusp medium width, daggerlike or rounded; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-3(4, 5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 26–29 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 32–36 cusps; cutting edge occupying 25% of length of tooth. Stomach and style sac equal sized; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented, except for scattered internal, grey granules, to dark grey-black. Snout light to dark grey-black. Foot, neck light to medium grey. Opercular lobe usually dark along inner edge, sometimes also along sides or all around. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally for most of length; pigment granules also sometimes scattered on base and lobe.

Ctenidial filaments, 22, strongly pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered posterior to middle of ctenidium. Renal gland longitudinal; kidney opening white, muscularized. Rectum broadly overlapping genital ducts.

Ovary 1.0–1.25 whorls, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 30G. Albumen gland with short pallial component. Capsule gland shorter, but as wide as albumen gland, sub-circular in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes forming a weak papilla, having short anterior extension. Coiled oviduct a small, posterior-oblique loop, preceded and overlapped by similar loop or strong twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, often with abrupt narrowing near mid-line, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, often poorly distinguished from bursa, 50% of bursa length, medium width, often shallowly embedded in albumen gland. Seminal receptacle small to medium-sized, pouchlike, overlapping or lateral (ventral side) to anterior portion of bursa.

Testis 2.0 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed bend, sometimes slightly reflexed. Penis (Figure 30H, I) medium-sized; base rectangular, smooth or weakly folded; filament medium length and width, tapering to point, straight or slightly oblique; lobe knoblike, slightly longer than filament, slightly oblique. Terminal gland small, narrow, rarely divided into two units, curved, transverse, largely on ventral surface. Penial gland small, slightly narrower than filament, filling proximal half of fil-

ament and sometimes extending slightly onto base. Small, slightly raised, distal ventral gland seen in single specimen. Penial duct straight, near outer edge.

**Type locality:** Spring, Hunts Canyon Ranch, Ralston Valley, Nye County, Nevada, T. 8 N, R. 46 E, SW  $\frac{1}{4}$  section 31 (Figure 50). Holotype, USNM 874876 (Figure 18K), collected by D. W. Sada, 8 November 1992; paratypes, USNM 860714. The type locality is a small rheocrene located in the middle of a pasture on a private ranch.

**Remarks:** This snail is contrasted with *P. turbatrix* above. Material collected from the type locality had a high incidence of trematode parasitism, which may be related to the occurrence of scalariform individuals in this sample.

**Material examined:** NEVADA. *Nye County:* Spring, Hunts Canyon Ranch, USNM 860714, USNM 874760, USNM 874876.—Spring, feeding pond at ranch house, Hunts Canyon Ranch, Ralston Valley, USNM 874767.—Sidehill Spring, (west) Stone Cabin Valley, T. 5 N, R. 47 E, SW  $\frac{1}{4}$  section 26, USNM 874769, USNM 874877.

*Pyrgulopsis ruinosa* Hershler, sp. nov.

Fish Lake Valley pyrg

(Figures 7A, 18M, 31A–C)

**Etymology:** From *ruinosus* (Latin), going to ruin; referring to the current status of this species.

**Diagnosis:** Medium-sized, with ovate-conic shell. Penis large, filament and lobe short. Penial ornament a large terminal gland, small Dg1; large, fused Dg2–Dg3; and large ventral gland.

**Description:** Shell (Figures 7A, 18M) usually ovate-conic, rarely sub-globose or narrow conic; width/height, 63–80%; height, 2.6–3.3 mm; width, 1.8–2.3 mm; whorls, 4.25–5.0. Protoconch 1.3 whorls, diameter 0.44 mm; initial whorl finely wrinkled, later portion becoming smooth. Teleoconch whorls medium convexity, sutures deeply impressed; shoulders well developed; body whorl slightly disjunct behind the aperture in larger specimens. Aperture ovate, usually disjunct. Inner lip thin, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, weakly sinuate. Umbilicus perforate. Periostracum tan.

Operculum ovate, amber, nuclear region darker; nucleus eccentric; dorsal surface weakly frilled; outer margin having weak rim. Attachment scar thick all around.

Radula 610  $\times$  115  $\mu\text{m}$ , with 60 rows of teeth. Central tooth 27  $\mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 5–7; central cusp broad, daggerlike; basal cusps small, sometimes accompanied by weak thickening on outside. Basal process often slightly shorter than lateral margins, V-shaped, basal sockets medium depth. Lateral tooth formula 2(3, 4)-1-3(4, 5); neck weakly flexed;

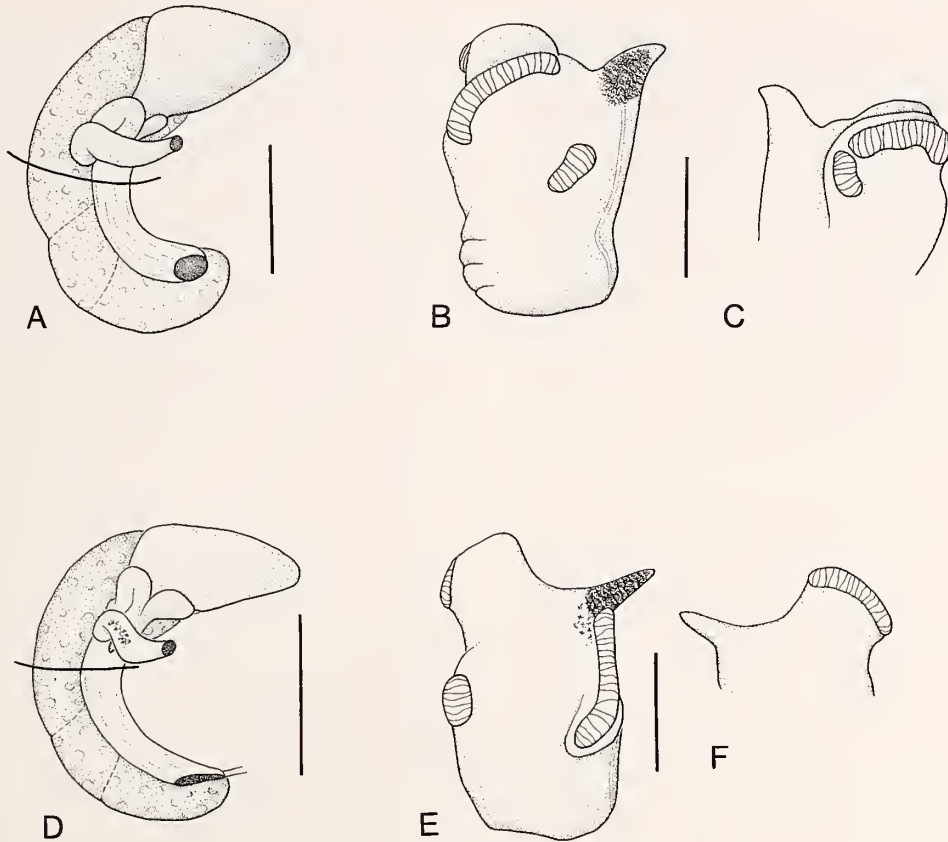


Figure 31

Genitalia of *Pyrgulopsis* species (A–C, *P. ruinosa*, USNM 860700; D–F, *P. sublata*, USNM 860724). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis.

outer wing 190% of cutting edge length. Inner marginal teeth with 20–28 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 24–35 cusps; cutting edge occupying 28% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or light grey-brown. Snout, foot unpigmented to dark grey-brown. Opercular lobe unpigmented or dark along inner edge, sometimes also darkly pigmented along sides. Neck unpigmented to medium grey-brown. Pallial roof, visceral coil light grey-brown to uniform black. Penial filament darkly pigmented internally.

Ctenidial filaments, 22, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered slightly posterior to middle of ctenidial axis. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 31A. Albumen

gland having medium pallial component. Capsule gland shorter and as wide as albumen gland, sub-circular in section; rectal furrow absent to well developed. Ventral channel moderately overlapping capsule gland; longitudinal fold well developed. Genital aperture a sub-terminal pore; anterior extension absent or weakly developed. Coiled oviduct a posterior-oblique loop preceded by prominent posterior twist or small coil. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix 50% as long as albumen gland, as wide as gland, broadly ovate to pyriform, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge near mid-line, medium length and width. Seminal receptacle small, pouchlike, overlapping anteriormost bursa, often positioned near ventral edge of albumen gland.

Testis 1.5 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland large, elongate bean-shaped, pallial portion medium, ovate in section. Proximal pallial vas deferens having well-developed,

reflexed loop. Penis (Figure 31B, C) large; base rectangular, often folded along inner edge; filament short, medium width, tapering to point, slightly oblique; lobe short, squarish, broad, slightly oblique. Terminal gland large, narrow, curving, transverse, largely on ventral surface. Dg1 small, rarely dotlike, absent, or fragmented into two units, usually longitudinal, medial or positioned slightly proximal to filament. Dg2 and Dg3 usually fused into single, large, curved unit (rarely fused with Dg1) transversely positioned near distal edge of lobe; gland sometimes accompanied by one to two small units positioned alongside (sometimes abutting or fused to) proximal edge. Ventral gland large, rarely absent or accompanied by second, dotlike unit; borne on prominent swelling, longitudinal-transverse, positioned near base of lobe. Penial duct straight, near outer edge.

**Type locality:** Spring, southwest of The Crossing, Fish Lake Valley, Esmeralda County, Nevada, T. 1 N, R. 36 E, SW  $\frac{1}{4}$  section 16 (Figure 50). Holotype, USNM 873407 (Figure 18M), collected by R. Hershler and D. Giuliani, 16 July 1988; paratypes, USNM 860700. The type locality, a small, thermal (26°C.) limnocrene, is the northernmost of a series of five springs on a large ranch (Figure 4C). Snails were collected in the shallow outflow, and were absent both in the spring pool and in other springs of this complex. This species has not been collected on subsequent visits to this now degraded area and is probably extinct.

**Remarks:** Although not closely similar to any congener, this species resembles *P. gibba* and a group of species found in the Owens Valley region in that its penis is relatively well ornamented with glands, but lacks a penial gland. *Pyrgulopsis ruinosa* differs from the above species in having a relatively large Dg1, long, fused Dg2–3, and short penial filament.

**Material examined:** NEVADA. *Esmeralda County:* Spring, southwest of The Crossing (Figure 4C), USNM 860700, USNM 873407.

*Pyrgulopsis sublata* Hershler, sp. nov.

Lake Valley pyrg

(Figures 7B, 12E, 18N, O, 31D–F)

**Etymology:** From *sublatus* (Latin), raised aloft; referring to the prominently raised or frilled opercular whorls characterizing this species.

**Diagnosis:** Medium-sized, with broadly to ovate-conic shell. Penis large, filament and lobe short. Penial ornament a large terminal gland, large Dg1, and small Dg2.

**Description:** Shell (Figures 7B, 18N, O) broadly to ovate-conic, width/height, 66–78%; height, 2.2–2.7 mm; width, 1.4–2.0 mm; whorls, 4.5–5.0. Protoconch 1.4

whorls, diameter 0.35 mm; surface smooth except for very weak wrinkling around apex and faint spiral striae on later portion. Teleoconch whorls medium to highly convex, shoulders weak or absent; sculpture including occasional faint spiral striae. Aperture ovate, adnate or slightly disjunct. Inner lip usually thin; columellar shelf very narrow or absent. Outer lip usually thin, orthocline or weakly prosocline, weakly sinuate. Umbilicus rimate or shallowly perforate. Periostracum tan.

Operculum (Figure 12E) ovate, multispiral, amber, nuclear region reddish; nucleus eccentric; dorsal surface strongly frilled; outer margin having weak rim. Attachment scar thick along most of perimeter, broadly so between nucleus and inner edge; whorl outlines strongly bulging.

Radula 645  $\times$  100  $\mu$ m, with 63 rows of teeth. Central tooth 22  $\mu$ m wide, with highly indented dorsal edge; lateral cusps, 7–9; central cusp rounded; basal cusps medium-sized, sometimes accompanied by weak thickening to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-5(6); neck weakly flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 26–32 cusps; cutting edge occupying 29% of length of tooth. Outer marginal teeth with 27–34 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to medium grey. Snout, foot light to medium grey. Opercular lobe having black smear all around. Neck unpigmented to medium grey. Pallial roof, visceral coil medium grey-brown to black, pigment not uniform. Penial filament and adjacent portion of base darkly pigmented.

Ctenidial filaments, 17, pleated; pericardium overlapping ctenidium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 31D. Albumen gland with medium-large (30–40%) pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two slightly or greatly overlapping posterior-oblique loops; proximal loop often weakly developed, usually having weak pigment streak on proximal arm. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix 67% as long and often as wide as albumen gland, elongate-pyriform, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at midline, medium length, medium width. Seminal receptacle small, pouchlike, overlapping anteriormost bursa, extending to edge of albumen gland.



Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland large, bean-shaped, pallial portion medium, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 31E, F) large, broadly rectangular, weakly folded or smooth; filament short, narrow, tapering to point, oblique; lobe short (usually as long as filament), square (rarely club-like), slightly oblique. Terminal gland large, narrow, rarely ovate or bifurcate; transverse, largely ventral. Dg1 extending from base of filament (sometimes slightly overlapping filament) along outer edge to medial position and then curving inward a short distance; proximal portion borne on low swelling; gland occasionally split into two similarly sized, abutting units. Dg2 small, ovate, medial (or slightly basal to middle of penis), borne along inner edge (often protruding slightly), usually longitudinal or slightly oblique, sometimes curving transversely toward Dg1. Penial duct straight, near outer edge.

**Type locality:** Wambolt Springs, Lake Valley, Lincoln County, Nevada, T. 9 N, R. 65 E, NE  $\frac{1}{4}$  section 23 (Figure 50). Holotype, USNM 874681 (Figure 18N), collected by R. Hershler and P. Hovingh, 26 June 1992; paratypes, USNM 860724. The type locality is a shallow, but broad (8 m) helocrene, slightly disturbed by livestock.

**Remarks:** Among the group of species whose penes have an elongate Dg1, *P. subblata* resembles several species from Verde River drainage (see Hershler & Landye, 1988) and some populations herein referred to *P. kolobensis* in also having a well-developed Dg2 along the inner edge of the penis. *Pyrgulopsis subblata* differs from these species in lacking a ventral gland on the penis and in having a very strongly frilled, multispiral operculum.

**Material examined:** NEVADA. *Lincoln County:* Wambolt Springs, Lake Valley, T. 9 N, R. 65 E, NE  $\frac{1}{4}$  section 23, USNM 860724, USNM 874681.

*Pyrgulopsis lockensis* Hershler, sp. nov.

Lockes pyrg

(Figures 7C, 12F, 14G–I, 19A, 32A–C)

**Etymology:** Referring to endemism of this species at Lockes, Duckwater Valley.

**Diagnosis:** Small, with sub-globose to ovate-conic shell. Penis large, filament very short, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 7C, 19A) sub-globose to ovate-conic, width/height, 80–93%; height, 1.6–1.9 mm; width, 1.4–1.6 mm; whorls, 3.25–4.5. Protoconch 1.2 whorls, diameter 0.29 mm, weakly wrinkled along inner edge near apex, later portion smooth, with a few weak spiral striations. Teleoconch whorls highly convex; shoulders narrow or absent. Aperture sub-circular, usually adnate, rarely disjunct.

Inner lip medium thickness, without columellar shelf. Outer lip thin, orthocone or slightly prosocline, weakly sinuate. Umbilicus perforate. Periostracum tan.

Operculum (Figure 12F) broadly ovate, light amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar thick all around.

Radula (Figure 14G–I)  $570 \times 90 \mu\text{m}$ , with 47 rows of teeth. Central tooth  $20 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 5–6; central cusp narrow, daggerlike; basal cusps medium-sized. Basal process U-shaped, basal sockets medium depth. Lateral tooth formula 3-1-3(4); neck weakly flexed; outer wing 190% of cutting edge length. Inner marginal teeth with 21–24 cusps, including large near basal cusp offset from others; cutting edge occupying 46% of length of tooth. Outer marginal teeth with 25–31 cusps; cutting edge occupying 29% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles, snout unpigmented or light grey-brown. Foot unpigmented or light grey-brown, darker along anterior edge. Opercular lobe black along inner edge. Neck unpigmented except for internal grey granules. Pallial roof, visceral coil usually light-medium grey-brown, rarely black, pigment usually darker on anterior mantle. Penis unpigmented.

Ctenidial filaments, 20, pleated; ctenidium overlapping pericardium posteriorly. Osphradium medium-sized, narrow, centered slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening white. Rectum broadly overlapping genital ducts.

Ovary a little less than 1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 32A. Albumen gland having very short pallial component. Capsule gland slightly shorter and narrower than albumen gland, sub-circular in section; rectal furrow weakly developed. Ventral channel overlapping capsule gland to medium extent; longitudinal fold well developed. Genital aperture a short slit opening near middle of capsule gland; anterior extension short. Coiled oviduct a tight, circular loop kinked proximally or at mid-length. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix medium length and width, narrowly-ovate, often curved, usually oblique, with 33% of length posterior to albumen gland, anterior edge often shallowly embedded in gland. Bursal duct originating from or near anterior edge at mid-line, short, medium width. Seminal receptacle very small, pouchlike, overlapping anteriormost portion of bursa, often shallowly embedded in albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 32B, C) large; base elongate, smooth, sometimes having sub-terminal bulge; filament very

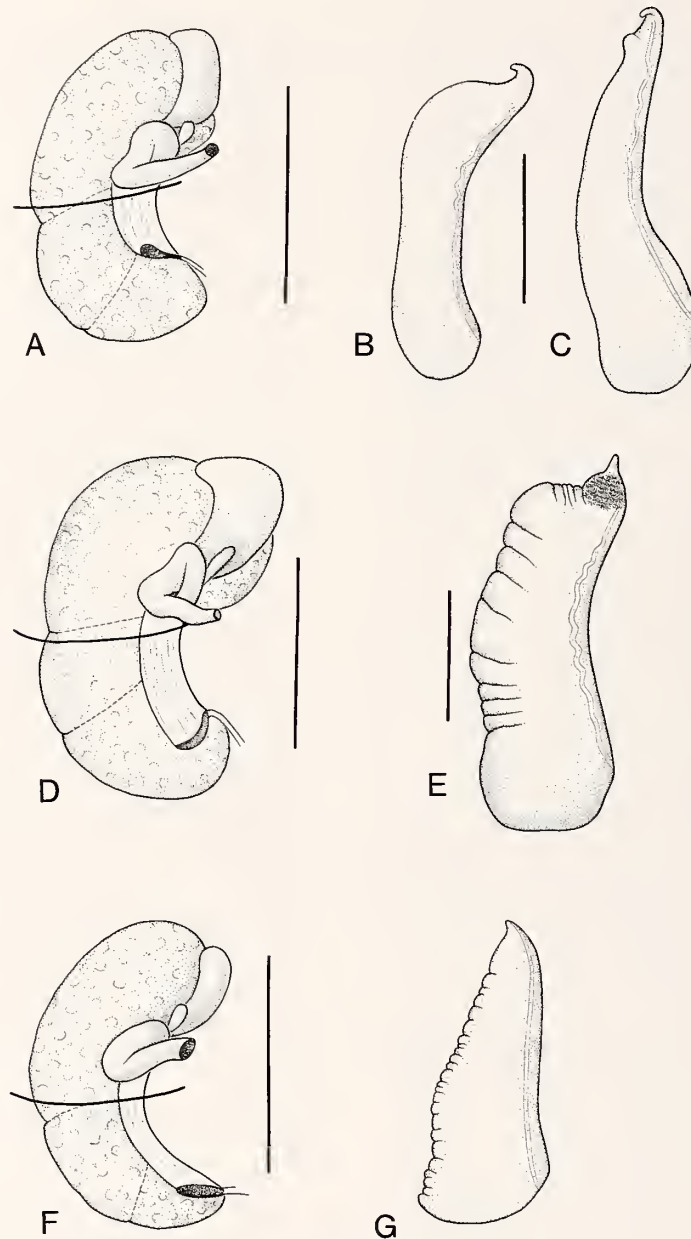


Figure 32

Genitalia of *Pyrgulopsis* species (A–C, *P. lockensis*, USNM 874879; D, E, *P. papillata*, USNM 860678; F, G, *P. carinata*, USNM 860680). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis.

short, narrow, usually tapering to point, longitudinal or slightly oblique, usually curved; lobe and glands absent. Penial duct weakly undulating distally, near outer edge.

**Type locality:** Spring, Lockes, Duckwater Valley, Nye County, Nevada, T. 8 N, R. 56 E, NE ¼ section 15 (Figure 50). Holotype, USNM 874779 (Figure 19A), collected by

D.W. Sada, 5 October 1992; paratypes, USNM 860679. The type locality is a large, thermal (30°C.) limnocrene.

**Remarks:** This snail, and two other species endemic to Duckwater Valley (*P. papillata*, *P. carinata*; described next), the northern extension of Railroad Valley, are united by small size, broadly conical shell with thin inner lip,

pale body pigmentation, simply coiled female oviduct, very small seminal receptacle; and simple, bladlike penis having very short filament; and probably compose a local radiation. This species is closely similar to *P. papillata* (which occurs a short distance to the north), as the snails share additional distinctive features of low trochoid or sub-globose shell, prominent spiral striae on the late protoconch, weakly undulating or straight pallial vas deferens, undulating penial duct, and sub-terminal or medial opening to the female genital duct. *Pyrgulopsis lockensis* differs from *P. papillata* in its weaker protoconch sculpture, smaller bursa copulatrix; and narrower penis, with less prominent filament lacking a distinct terminal papilla.

**Material examined:** NEVADA. *Nye County*: Spring, Lockes, USNM 860679, USNM 873168, USNM 874017, USNM 874779, USNM 874879.

*Pyrgulopsis papillata* Hershler, sp. nov.

Big Warm Spring pyrg

(Figures 7D, 11E, 19B, 32D, E)

**Etymology:** From *papillatus* (Latin), papillate, referring to the prominent terminal papilla on the penis of this species.

**Diagnosis:** Small, with sub-globose shell. Penis large, filament very short, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 7D, 19B) sub-globose; width/height, 80–92%; height, 1.8–2.2 mm; width, 1.6–1.9 mm; whorls, 3.25–3.75. Protoconch (Figure 11E) 1.2 whorls, diameter 0.29 mm, initial 0.75 whorl sculptured with irregular, coarse wrinkles, sculpture coalescing in later portion to form a few, widely spaced spiral elements. Teleoconch whorls medium to highly convex, shoulders weakly developed or absent. Aperture broadly ovate, adnate or slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, orthocone or slightly prosocline, weakly sinuate. Umbilicus perforate. Periostracum light tan.

Operculum ovate, light amber; nucleus slightly eccentric; dorsal surface frilled. Attachment scar thick almost all around, especially so between nucleus and inner edge and along inner edge.

Radula  $535 \times 86 \mu\text{m}$ , with 57 rows of teeth. Central tooth  $20 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 6–7; central cusp narrow, daggerlike, basal cusps small. Basal process broad, almost U-shaped, basal sockets medium depth. Lateral tooth formula 3(4, 5)-1-4(5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 24–28 cusps; cutting edge occupying 35% of length of tooth. Outer marginal teeth with 25–29 cusps; cutting edge occupying 24% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger and posterior chamber; stomach caecum very small or absent.

Animal generally very pale. Cephalic tentacles, snout, neck, foot usually unpigmented, rarely light to medium brown. Opercular lobe often having distinctive black streak along inner edge. Pallial roof, visceral coil light to medium brown or red; testis often black. Penial filament darkly pigmented internally.

Ctenidial filaments, 30, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland longitudinal; kidney opening grey. Rectum broadly overlapping genital ducts.

Ovary 1.0 whorl, filling 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 32D. Albumen gland without pallial component. Capsule gland as long as, but slightly narrower than albumen gland, sub-circular in section, with short component behind pallial wall; rectal furrow weakly developed. Ventral channel narrowly overlapping capsule gland; longitudinal fold well developed. Genital aperture a sub-terminal slit having short anterior extension. Coiled oviduct a tight circular loop, usually kinked proximally or in mid-section. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, narrow, pyriform, oblique-transverse, pressed against edge of albumen gland with 33% of length posterior to gland. Bursal duct originating at or near anterior edge at mid-line, short, medium width, slightly embedded in albumen gland along ventral edge. Seminal receptacle very small, narrow, overlapping anterior bursa near ventral edge.

Testis 1.25 whorls, filling most of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland ovate, pallial portion short, ovate in section. Proximal pallial vas deferens having weak bend or series of undulations. Penis (Figure 32E) large; base rectangular-elongate, often distally swollen, folded along inner edge; filament very short, medium width, bulbous, sub-longitudinal, terminating in narrow papilla; lobe absent or a very short bulge; glands absent. Penial duct near outer edge, undulating.

**Type locality:** Big Warm Spring, Duckwater Valley, Nye County, Nevada, T. 13 N, R. 56 E, SE  $\frac{1}{4}$  section 32. Holotype, USNM 873185 (Figure 19B), collected by J.J. Landye, 3 September 1973; paratypes, USNM 860678. The type locality is a large, thermal (31°C.) limnocrone (Figure 4D), which flows into a canal system, located on the Duckwater Indian Reservation. Snails were collected from aquatic vegetation (Bladderwort) in the spring pool.

**Remarks:** This species is compared to *P. lockensis* above. The distribution of this snail is shown in Figure 50.

**Material examined:** NEVADA. *Nye County*: Big Warm Spring (Figure 4D), USNM 860678, USNM 873185, USNM 874772.—Little Warm Spring, Duckwater Valley,

T. 12 N, R. 56 E, NE ¼ section 5, USNM 883974, USNM 892016.

*Pyrgulopsis carinata* Hershler, sp. nov.

Carinate Duckwater pyrg

(Figures 7E, 19C, 32F, G)

**Etymology:** From *carinatus* (Latin), keeled; referring to the prominently carinate late teleoconch whorls on shells of this species.

**Diagnosis:** Medium-sized, with ovate-conic, distinctly carinate shell. Penis medium-sized; filament very short, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 7E, 19C) ovate-conic, width/height, 78–89%; height, 1.8–2.5 mm; width, 1.6–2.0 mm; whorls, 3.5–4.0. Protoconch 1.1 whorls, diameter 0.28 mm, earliest portion finely wrinkled, otherwise smooth. Teleoconch whorls flat or slightly convex, shoulders broad, forming strong carina on final 2.5 whorls. Aperture ovate, adnate or slightly disjunct. Inner lip thick, without columellar shelf. Outer lip thin, orthocline, without sinuation. Umbilicus perforate to broadly open. Periostracum light tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface weakly frilled; outer margin having rim. Attachment scar thick all around.

Radula  $590 \times 85 \mu\text{m}$ , with 62 rows of teeth. Central tooth  $24 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 5–6; central cusp medium width, dagger-like; basal cusps small. Basal tongue broad V- or U-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 24–28 cusps; cutting edge occupying 39% of length of tooth. Outer marginal teeth with 23–31 cusps; cutting edge occupying 28% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber slightly larger than posterior chamber; stomach caecum absent or very small.

Cephalic tentacles unpigmented or with medium brown stripe near bases. Snout, foot unpigmented. Opercular lobe often having black streak along inner edge and sides, otherwise unpigmented. Neck unpigmented or with scattered internal grey granules. Pallial roof, visceral coil unpigmented to medium brown-black; pigment usually lighter on pallial roof. Penial filament sometimes darkly pigmented internally.

Ctenidial filaments, 23, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland longitudinal; kidney opening grey. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5–0.75 whorl, filling more than 50% of diges-

tive gland behind stomach, abutting edge of stomach anteriorly. Distal female genitalia shown in Figure 32F. Albumen gland with very short or no pallial component. Capsule gland shorter and narrower than albumen gland, ovate in section; rectal furrow absent. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit with short anterior extension. Coiled oviduct a tight, circular loop. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix short, narrow, narrowly ovate-tubular, longitudinal, extending to posterior edge of albumen gland; positioned along ventral edge of gland, with portion (rarely entirely) extending onto right side. Bursal duct originating from anterior edge at mid-line, often poorly distinguished from bursa, shorter than bursa, medium width. Seminal receptacle very small, pouchlike, overlapping anteriormost bursa of proximal bursal duct.

Testis 1.0 whorl, filling more than 50% of digestive gland behind stomach, partly overlapping posterior stomach chamber. Prostate gland bean-shaped, entirely visceral or with very short pallial portion, ovate in section. Proximal pallial vas deferens straight or with very small bend. Penis (Figure 32G) medium-sized; base rectangular, usually folded along inner edge, slightly narrowed proximally, distally tapering; filament weakly distinguished from base, very short, medium width, strongly tapered, terminating in narrow, pointed papilla, longitudinal; lobe and glands absent. Penial duct straight, near outer edge.

**Type locality:** Little Warm Spring, Duckwater Valley, Nye County, Nevada, T. 12 N, R. 56 E, NE ¼ section 5 (Figure 51). Holotype, USNM 883975 (Figure 19C), collected by J.J. Landye, 3 September 1973; paratypes, USNM 860680. The type locality is a large, thermal (30°C.) limnocrone on the Duckwater Indian Reservation.

**Remarks:** As mentioned above, this species shares unusual features with *P. papillata* (with which it co-occurred in Little Warm Spring) and *P. lockensis*. *Pyrgulopsis carinata* differs from the above in its strongly carinate shell, smoother protoconch (lacking any spiral striae), simply tapering penis, and more distal capsule gland opening. This snail was collected from the type locality in 1973. During two recent visits to this spring the species could not be found (although *P. papillata* still is present), and it is likely extinct.

**Material examined:** NEVADA. *Nye County:* Little Warm Spring, USNM 860680, USNM 883975.

*Pyrgulopsis aloba* Hershler, sp. nov.

Duckwater pyrg

(Figures 7F, 19D, E, 33A, B)

**Etymology:** From *lobus* (Latin), projection; referring to absence of a lobe on the penis of this species.

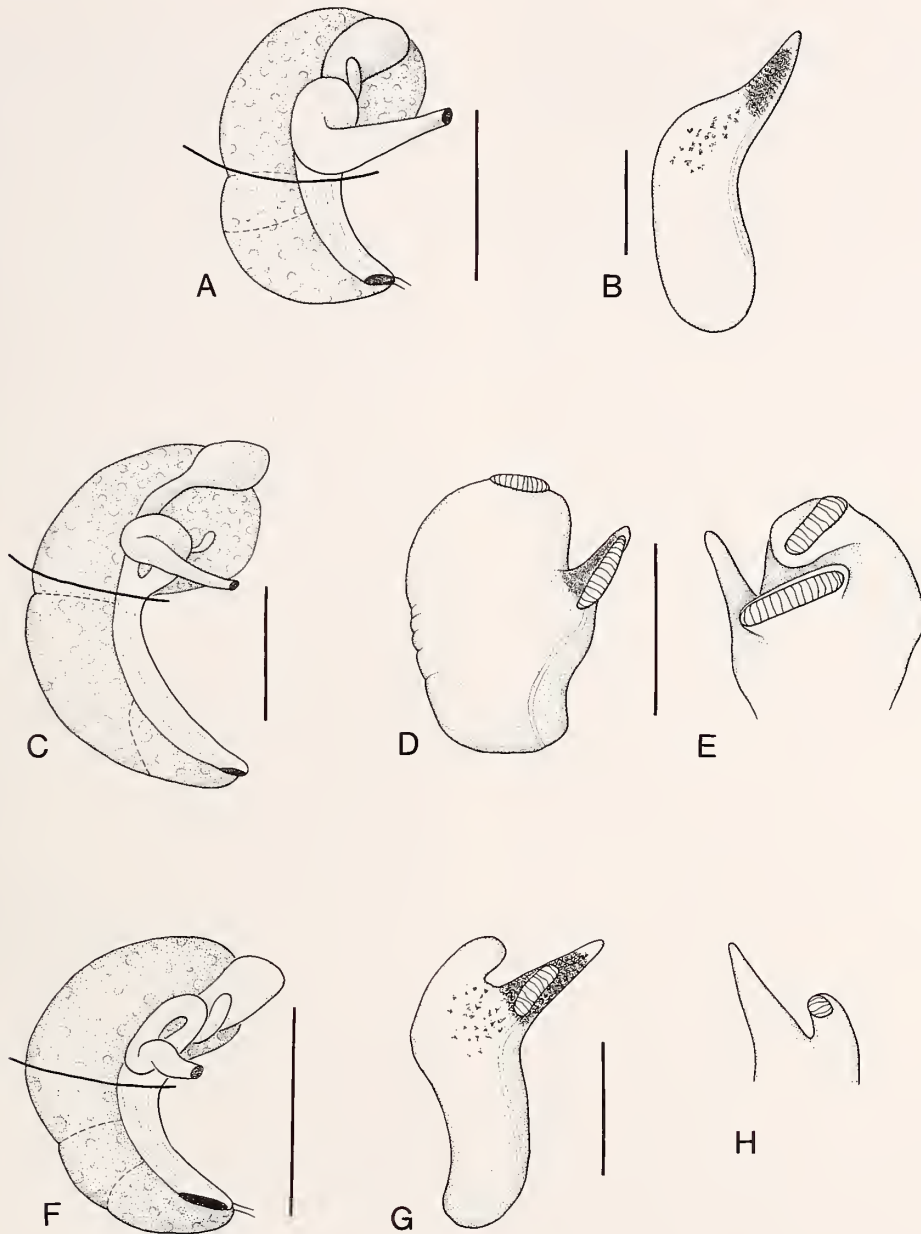


Figure 33

Genitalia of *Pyrgulopsis* species (A, B, *P. aloba*, USNM 860681; C–E, *P. villacampae*, USNM 860712; F–H, *P. anatina*, USNM 860710). A, B. Bar = 0.25 mm. C–H. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. aloba* as penial ornament absent).

**Diagnosis:** Small, with sub-globose to ovate-conic shell. Penis medium-sized; filament medium length, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 7F, 19D, E) sub-globose to ovate-conic, apex usually eroded, width/height, 80–96%; height, 1.0–1.9 mm; width, 1.0–1.7 mm; whorls, 2.5–4.0.

Protoconch 1.25 whorls, diameter 0.25 mm, finely wrinkled, but becoming near smooth near teleoconch border. Teleoconch whorls moderately convex, shoulders weak, but sometimes forming pronounced sub-sutural angulation on body whorl. Aperture ovate, angled above, usually adnate. Inner lip thick, sometimes forming narrow

columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus absent-rimate. Periostracum light brown-tan.

Operculum ovate, amber, reddish in nuclear region; nucleus eccentric; dorsal surface frilled. Attachment scar sometimes thick along inner edge.

Radula  $418 \times 63 \mu\text{m}$ , with 62 rows of teeth. Central tooth  $14 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 5–7; central cusp medium width, dagger-like; basal cusps medium-sized. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-5(6); neck weakly flexed; outer wing 220% of cutting edge length. Inner marginal teeth with 23–26 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 27–29 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum very small or absent.

Cephalic tentacles light to medium grey-brown; pigment often concentrated as short longitudinal strip proximally. Snout light to dark grey-brown. Foot light to medium grey. Inner edge of opercular lobe black. Neck unpigmented to medium grey. Pallial roof, visceral coil dark brown-black. Penial filament darkly pigmented internally, distal portion of base having scattered black granules.

Ctenidial filaments, 11, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, ovate, positioned centrally or slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling 50% or slightly more of digestive gland behind stomach, overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 33A. Albumen gland without pallial component. Capsule gland slightly shorter and narrower than albumen gland, ovate in section; rectal furrow deep. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a single, tight circular loop. Oviduct and bursal duct joining slightly behind pallial wall. Oviduct opening to albumen gland at pallial wall. Bursa copulatrix short, narrow, narrowly ovate, longitudinal, extending to or just proximal to edge of gland. Bursal duct originating from anterior edge at mid-line, close to oviduct, slightly shorter than bursa, medium width. Seminal receptacle small, pouch-like, overlapping anterior portion of bursa.

Testis 0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber anteriorly. Prostate gland bean-shaped, pallial portion very short; narrowly ovate in section. Proximal pallial vas deferens having small bend. Penis (Figure 33B) medium-sized; base rectangular, lacking folds; filament medium length and width, tapering to point, slightly oblique; lobe and glands absent. Penial duct very close to outer edge, straight.

**Type locality:** Spring, northwest of Duckwater, Duckwater Valley, Nye County, Nevada, T. 13 N, R. 56 E, center section 31. Holotype, USNM 883847 (Figure 19D), collected by R. Hershler and P. Hovingh, 12 July 1994; paratypes, USNM 860681. The type locality is a small rheocene on the Duckwater Indian Reservation.

**Remarks:** This species resembles some of the other locally endemic forms from Duckwater Valley (especially *P. carinata*) in having a simple penis, but differs in having much stronger body pigment, larger oviduct coil, more anteriorly positioned bursa copulatrix, and smooth penis with larger filament. Snails collected at the head of a small spring (USNM 873187) about 2.0 km southeast of the type locality closely conform to *P. aloba* in all respects, while the outflow of this same spring yielded much larger, taller snails (USNM 873189) having highly stunted penes that otherwise conformed to those of this species. Additional collections will have to be made to better evaluate this interesting dimorphism. The distribution of this species is shown in Figure 51.

**Material examined:** NEVADA. *Nye County:* Spring, northwest of Duckwater, USNM 860681, USNM 883847.—Spring (source), east-southeast of Duckwater, Duckwater Valley, T. 12 N, R. 56 E, SW  $\frac{1}{4}$  section 5, USNM 873187.—Spring (outflow), east-southeast of Duckwater, Duckwater Valley, T. 12 N, R. 56 E, SW  $\frac{1}{4}$  section 5, USNM 873189.

*Pyrgulopsis villacampae*, Hershler, sp. nov.

Duckwater Warm Springs pyrg

(Figures 7G, 13A, 19F, G, 33C–E)

**Etymology:** Named after Yolanda Villacampa, who assisted with much of the laboratory work associated with this project.

**Diagnosis:** Medium-sized, with trochiform-neritiform shell. Penis large, filament and lobe medium length. Penial ornament a medium-sized terminal gland, large penial gland, and large ventral gland.

**Description:** Shell (Figures 7G, 19F, G) trochiform-neritiform, apex often eroded, width/height, 81–94%; height, 2.5–3.7 mm; width, 2.3–3.1 mm; whorls, 3.5–4.5. Protoconch 1.2 whorls, diameter 0.33 mm; initial 0.75 whorl sculptured with widely separated, raised wrinklelike elements, later portion smooth. Teleoconch whorls medium-highly convex, sometimes having weak sub-sutural angulation on body whorl. Aperture broadly ovate, usually adnate. Inner lip thin, without columellar shelf. Outer lip thin, prosocline, strongly sinuate. Umbilicus rimate-narrow. Periostracum tan.

Operculum (Figure 13A) broadly ovate, light amber; nucleus sub-central; dorsal surface frilled; outer margin

having weak rim. Attachment scar slightly thickened between nucleus and inner edge.

Radula 1.09 mm  $\times$  130  $\mu$ m, with 63 rows of teeth. Central tooth 33  $\mu$ m wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp narrow, daggerlike; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed; outer wing 130% of cutting edge length. Inner marginal teeth with 23–26 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 27–29 cusps; cutting edge occupying 24% of length of tooth. Stomach as long or slightly shorter than style sac; anterior chamber slightly larger; stomach caecum very small.

Cephalic tentacles unpigmented to medium brown. Snout unpigmented to dark brown-black. Foot unpigmented to medium brown, sole often grey. Opercular lobe unpigmented or brown along sides. Neck unpigmented to light brown. Pallial roof, visceral coil light to dark brown, red, or black, often uniformly pigmented. Penial filament darkly pigmented internally.

Ctenidium very wide; filaments, 43, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland oblique; kidney opening grey. Rectum broadly overlapping pallial oviduct, scarcely or not overlapping prostate gland.

Ovary 1.0–1.25 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Distal female genitalia shown in Figure 33C. Albumen gland having short or no pallial component. Capsule gland longer (sometimes markedly so), but narrower than albumen gland, anterior section markedly distal, sub-circular in section, rectal furrow weak. Ventral channel narrowly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit, sometimes slightly separated, lacking an anterior expansion. Coiled oviduct a single, tight circular loop, sometimes weakly kinked proximally. Oviduct and bursal duct joining slightly behind pallial wall. Oviduct opening to albumen gland at pallial wall. Bursa copulatrix short, narrow, sub-globular to ovate, longitudinal, with 33–50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, long, narrow. Seminal receptacle very small, pouchlike, positioned well anterior to bursa near ventral edge of albumen gland.

Testis 1.25 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland very small, ovate, pallial portion short, ovate in section. Proximal pallial vas deferens broadly arched (angling toward rectum). Penis (Figure 33D, E) large; base rectangular, sometimes near square, inner edge weakly folded, often expanded distally; filament medium length, narrow, tapering to point, slightly oblique; lobe slightly shorter than base, broadly triangular, longitudinal. Terminal gland medium-sized,

narrow, usually transverse, ventral, but sometimes curving to dorsal surface. Penial gland filling most of length of filament, almost as wide as filament. Ventral gland large, borne on pronounced swelling, traversing penis near base of filament. Penial duct straight, near outer edge.

**Type locality:** Little Warm Spring, Duckwater Valley, Nye County, Nevada, T. 12 N, R. 56 E, NE  $\frac{1}{4}$  section 5. Holotype, USNM 873191 (Figure 19F), collected by J.J. Landye, 3 September 1973; paratypes, USNM 860712. Snails were collected from rocks in the 1 m deep outflow of this spring.

**Remarks:** This unusual thermal endemic is not closely similar to other species of the region. Although the penial glands of *P. villacampae* conform, in general, to that of widespread *P. kolobensis*, this snail otherwise differs in its broader shell; narrower, more pointed central cusps on the central radular teeth; broader penis, smaller sperm pouches, and more anteriorly positioned seminal receptacle (relative to bursa copulatrix). The distribution of this species is shown in Figure 51.

**Material examined:** NEVADA. *Nye County:* Little Warm Spring, USNM 860712, USNM 873191, USNM 874759, USNM 892015.—Big Warm Spring, Duckwater Valley (Figure 4D), T. 13 N, R. 56 E, SE  $\frac{1}{4}$  section 32, USNM 883938.

*Pyrgulopsis anatina* Hershler, sp. nov.

Southern Duckwater pyrg

(Figures 7H, 19H, I, 33F–H)

**Etymology:** From *anatinus* (Latin), relating to ducks; referring to endemism of this species in Duckwater Valley.

**Diagnosis:** Medium-sized, with broadly to ovate-conic shell. Penis medium-sized; filament and lobe medium length. Penial ornament a small terminal gland, and medium-sized penial gland.

**Description:** Shell (Figures 7H, 19H, I) broadly to ovate-conic, width/height, 71–81%; height, 2.3–2.9 mm; width, 1.8–2.3 mm; whorls, 4.25–4.75. Protoconch 1.25 whorls, diameter 0.35 mm; surface smooth except for very weak wrinkling along inner edge near apex. Teleoconch whorls medium to highly convex, shoulders weakly developed to broad. Aperture ovate, usually adnate, sometimes slightly disjunct. Inner lip complete, slightly thickened, without columellar shelf. Outer lip thin, orthocone or weakly prosocline, without sinuation. Umbilicus rimate to shallowly perforate. Periostracum tan.

Operculum ovate, amber; nucleus slightly darker hue; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 570  $\times$  85  $\mu$ m, with 59 rows of teeth. Central tooth 22  $\mu$ m wide, with highly indented dorsal edge; lat-

eral cusps, 6–10; central cusp narrow, dagger- or spoon-like; basal cusps sometimes accompanied by thickening to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3(4, 5)-1-4(5, 6); neck weakly on medium-flexed; outer wing 180% of cutting edge length. Inner marginal teeth with 25–30 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 27–42 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light to medium grey-brown, pigmented often concentrated proximally. Snout light to dark grey-brown, sometimes almost black. Foot light to medium grey-brown. Neck light to medium grey-brown. Pallial roof, visceral coil dark brown-black. Penial filament darkly pigmented except for distalmost portion; black pigment granules scattered on distal penis.

Ctenidial filaments, 22, pleated; ctenidium overlapping pericardium proximally. Osphradium small, narrow, centered posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 1.0 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Distal female genitalia shown in Figure 33F. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, sub-circular in section; rectal furrow well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a broad, posterior-oblique loop preceded by well-developed posterior-oblique twist or small coil. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix medium length and width, ovate or weakly pyriform, longitudinal, with 33% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, short to almost as long as bursa, medium width, sometimes poorly distinguished from bursa. Seminal receptacle small to medium-sized, narrow pouch-shaped, overlapping or lateral to anterior half of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion medium-large (up to 40%), narrowly ovate in section. Proximal pallial vas deferens having well-developed loop; duct broad. Penis (Figure 33G, H) medium-sized (stunted in parasitized animals); base narrowly rectangular, smooth; filament medium length and width, tapering to point, longitudinal or slightly oblique; lobe slightly shorter to as long as filament, narrow, knoblike, longitudinal. Terminal gland small, ovate, transverse, ventral. Penial gland filling proximal 67% of filament, slightly narrower than filament. Penial duct straight, near outer edge.

**Type locality:** Spring, southeast of Old Collins Spring,

Duckwater Valley, Nye County, Nevada, T. 12 N, R. 56 E, NE  $\frac{1}{4}$  section 20 (Figure 51). Holotype, USNM 883848 (Figure 19H), collected by R. Hershler and P. Hovingh, 12 July 1994; paratypes, USNM 860710. The type locality is a small rheocene.

**Remarks:** This species is contrasted with *P. marcida* (above) and also with *P. serrata* (below). The single sample of this species contained few males, and only one specimen had a fully extended penis.

**Material examined:** NEVADA. *Nye County:* Spring, southeast of Old Collins Spring, USNM 860710, USNM 883848.

*Pyrgulopsis planulata* Hershler, sp. nov.

Flat-topped Steptoe pyrg

(Figures 7I, 13B, 15A–C, 19J, 34A–C)

**Etymology:** From *planus* (Latin), flat; *ulus*, diminutive suffix; referring to the small sub-discoidal shell of this species.

**Diagnosis:** Small, with highly eroded shell apex, remaining portion sub-globular to discoidal. Penis medium-sized, filament medium length, lobe very short. Penial ornament of small terminal gland, very small Dg1, and small Dg2.

**Description:** Shell (Figures 7I, 19J) apex highly eroded, remaining portion sub-globular to discoidal, width/height, 92–108%; height, 1.1–1.4 mm; width, 1.1–1.5 mm; whorls, 2.0–3.0. Protoconch eroded. Body whorl medium convexity, sometimes weakly angulate below periphery, shoulder weakly developed. Aperture ovate, weakly angled above; usually adnate, larger specimens sometimes slightly disjunct. Inner lip slightly thickened in larger specimens; columellar shelf often covering most of umbilical region. Outer lip thin (slightly thickened in larger specimens), strongly prosocline, without sinuation. Shell anomphalous or with narrowly rimate umbilicus; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum (Figure 13B) broadly ovate, multispiral, amber, nuclear region reddish; nucleus eccentric; dorsal surface frilled. Attachment scar thick along most of perimeter; whorl edges bulging.

Radula (Figure 15A–C) 550 × 90  $\mu$ m, with 65 rows of teeth. Central tooth 16  $\mu$ m wide, with highly indented dorsal edge; lateral cusps, 3–6 (dorsally fused); central cusps broad, daggerlike (often with jagged edge), basal cusps absent, although small swelling often present in area. Basal tongue V-shaped, longer than lateral angles, basal sockets shallow. Lateral margins narrow, strongly flared. Lateral tooth formula 4(5)-1-4(5); neck well flexed; outer wing 260% of cutting edge length. Inner marginal teeth with 24–26 cusps; cutting edge occupying 28% of length of tooth. Outer marginal teeth with 27–30



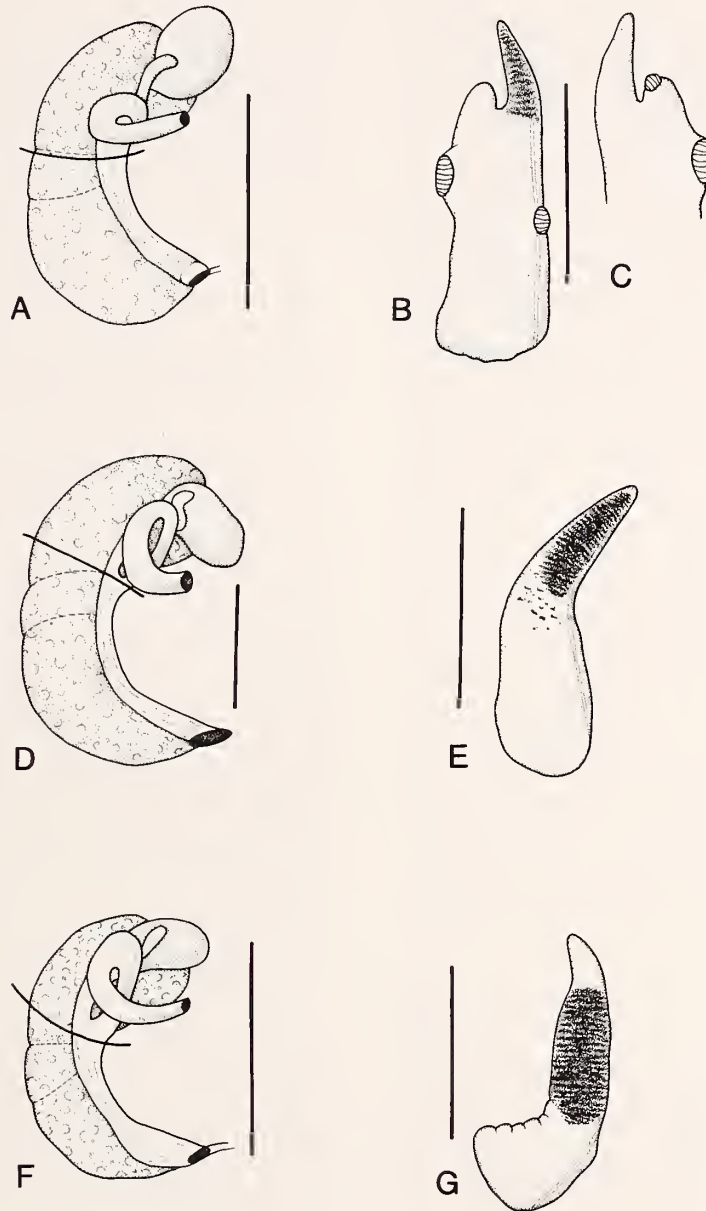


Figure 34

Genitalia of *Pyrgulopsis* species (A–C, *P. planulata*, USNM 860686; D, E, *P. sulcata*, USNM 860683; F, G, *P. orbiculata*, USNM 860682). A–C. Bars = 0.5 mm. D. Bar = 0.25 mm. E. Bar = 0.5 mm. F. Bar = 0.5 mm. G. Bar = 0.25 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. sulcata* and *P. orbiculata* as penial ornament absent).

cusps; cutting edge occupying 20% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout dark brown. Foot, neck medium to dark brown. Opercular lobe dark along inner edge, often all around, central zone unpigmented. Pallial roof, visceral coil uniform black. Penial filament darkly

pigmented internally along most of length; portion of base adjacent to filament lightly to darkly pigmented.

Ctenidial filaments, 13; ctenidium connected to pericardium by short efferent vein. Osphradium small, narrow, positioned posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling more than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 34A. Albumen gland without pallial component. Capsule gland longer and as wide as albumen gland, having short pallial component, sub-globular in section, rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a short, terminal slit, mounted on weakly raised papilla, with short anterior extension. Coiled oviduct a tight circular or posterior-oblique loop. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix medium length and width, ovate, usually longitudinal (sometimes oblique), 50–67% of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line, medium length and width. Seminal receptacle small, pouchlike, often folded, overlapping anterior portion of bursa.

Testis 0.75–1.0 whorl, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland broadly ovate, pallial portion short, ovate in section. Proximal pallial vas deferens weakly looped. Penis (Figure 34B, C) medium-sized; base rectangular, weakly folded or smooth; filament medium length and width, tapering to point, longitudinal; lobe very short, longitudinal or slightly oblique, narrowly rounded. Terminal gland small, ovate, transverse, ventral. Dg1 very small, ovate, slightly raised, longitudinal, positioned along inner edge medially. Dg2 small, ovate, borne on distal expansion or lobelike swelling (lateral to edge of penis), positioned slightly proximal to lobe, largely or entirely ventral. Penial duct straight, very close to outer edge.

**Type locality:** Spring, northwest of Clark Spring, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, NW ¼ section 20 (Figure 51). Holotype, USNM 892023 (Figure 19J), collected by R. Hershler and P. Hovingh, 9 May 1995; paratypes, USNM 860686. The type locality is one of a series of small, thermal (23.3°C.) rheocrenes which enter an irrigation ditch on a private ranch. These springs also harbor an undescribed species of *Tryonia*.

**Remarks:** This snail and four other species are locally endemic to a large wetland near the southeast corner of Steptoe Valley. These species share numerous unusual features suggesting that they compose a local radiation, including small size, squat shell with columellar shelf and/or excavated umbilical region, strong protoconch sculpture, frilled operculum; deeply notched central radular teeth with attenuate, flared margins, long basal tongue, shallow sockets, fused lateral cusps, broad central cusps; long wings on lateral teeth, short cutting edges of marginal teeth, well posterior position of bursa copulatrix, simple oviduct coil, and capsule gland opening frequently developed as a papilla. *Pyrgulopsis planulata* differs from other members of this group by its unique pattern

of penial ornament, consisting of small terminal gland, Dg1 and Dg2.

**Material examined:** NEVADA. *White Pine County:* Spring, northwest of Clark Spring, USNM 860686, USNM 883985, USNM 892023, USNM 892026.

*Pyrgulopsis sulcata* Hershler, sp. nov.

Southern Steptoe pyrg

(Figures 7J, 11F, 19K, 34D, E)

**Etymology:** From *sulcatus* (Latin), furrowed; referring to the excavated shell umbilical region typical of this species.

**Diagnosis:** Small, with low-trochoid to ovate-conic shell. Penis medium-sized, bladelike, filament medium length, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 7J, 19K) low trochoid to ovate conic, apex usually eroded, parasitized specimens often cylindrical, width/height, 79–91%; height, 1.2–1.4 mm; width, 1.0–1.2 mm; whorls, 4.0–4.5. Protoconch (Figure 11F) 1.1 whorls, diameter 0.24 mm, coarsely wrinkled, with sculpture weakening slightly near teleoconch border. Teleoconch whorls weakly convex, shoulders well developed, narrow. Aperture ovate, adnate. Inner lip complete, slightly thickened, often having narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus absent or rimate; umbilical region often excavated and bordered by adaxial ridge. Periostracum light tan.

Operculum ovate, reddish; nucleus eccentric; dorsal surface weakly frilled near inner edge. Attachment scar broadly thickened between nucleus and inner edge.

Radula 420 × 66 μm, with 73 rows of teeth. Central tooth 11 μm wide, with highly indented dorsal edge; lateral cusps, 4–7, often fused dorsally; central cusp narrow, daggerlike; basal cusps usually absent, sometimes present as very small, nublike vestiges. Basal tongue V-shaped, extending well below lateral angles; basal sockets shallow. Lateral margins very narrow, strongly flared. Lateral tooth formula 5(6)-1-6(7); neck weakly flexed; outer wing 250% of cutting edge length. Inner marginal teeth with 27–30 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–28 cusps; cutting edge occupying 23% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles unpigmented to medium grey-brown. Snout medium to dark grey-brown. Foot light to medium grey-brown. Opercular lobe dark along inner edge, sometimes all around. Neck unpigmented to medium grey-brown. Pallial roof, visceral coil uniformly black. Penial filament darkly pigmented internally, pigment usually also present on distal portion of base.

Ctenidium narrow; filaments, 11, without pleats; cte-

nidium connected to pericardium by short efferent vessel. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling 50% of digestive gland behind stomach, abutting or slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 34D. Pallial albumen gland very short or absent. Capsule gland longer, narrower than albumen gland, sub-circular in section, proximal section well posterior; rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit, loosened from capsule gland, almost papillalike, anterior extension absent. Coiled oviduct a tight circular or narrow U-shaped loop. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal or slightly oblique (anterior edge dorsal), with short section posterior to gland. Bursal duct originating from anterior edge at mid-line, slightly shorter than bursa, medium width, slightly embedded in albumen gland. Seminal receptacle small, narrow, sometimes folded, overlapping anterior portion of bursa.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland bean-shaped, pallial portion medium, narrowly ovate in section. Proximal pallial vas deferens straight or with weak bend or undulation. Penis (Figure 34E) medium-sized; base narrowly rectangular, lacking folds, weakly distinguished distally from filament; filament slightly shorter and narrower than base, tapering to rounded tip, longitudinal or slightly oblique; lobe and glands absent. Penial duct straight, very close to outer edge.

**Type locality:** Springs, north of Grass Springs, Steptoe Valley, White Pine County, Nevada, T. 19 R, R. 63 E, NW ¼ section 8. Holotype, USNM 874326 (Figure 19K), collected by R. Hershler, 5 August 1991; paratypes, USNM 860683. The type locality is a small, marshy rheocrene whose outflow has been dug out to form a canal (Figure 4E).

**Remarks:** This snail closely resembles *P. orbiculata* (described below), which occurs just to the north, but its shell has less rounded whorls with deeper sutures, stronger shoulders, and a broader columellar shelf. In addition, *P. sulcata* differs in the nearly smooth dorsal surface of the operculum, weaker development of basal cusps on the central radular teeth, and shorter penial filament. The distribution of this species is shown in Figure 51.

**Material examined:** NEVADA. *White Pine County:* Springs, north of Grass Springs (Figure 4E), USNM 860683, USNM 874326.—Spring, northwest of Clark Spring, Steptoe Valley, T. 19 N, R. 63 E, NW ¼ section 20, USNM 883427, USNM 883894, USNM 892022.

*Pyrgulopsis orbiculata* Hershler, sp. nov.

Sub-globose Steptoe Ranch pyrg

(Figures 7K, 19L, 34F, G)

**Etymology:** From *orbis* (Latin), circle (coupled with diminutive suffix); referring to the small, sub-globose shell of this species.

**Diagnosis:** Small, with globose shell. Penis small, blade-like; filament long, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 7K, 19L) sub-globose, width/height, 81–96%; height, 1.1–1.3 mm; width, 1.0–1.2 mm; whorls, 3.75–4.25. Protoconch 1.2–1.25 whorls, diameter 0.25 mm, coarsely wrinkled, with sculptured weakening slightly near teleconch boundary. Teleconch whorls highly convex, often weakly angled at the periphery, shoulders absent or weak and narrow. Aperture broadly ovate, angled above, usually adnate. Inner lip slightly thickened, usually having narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate to perforate, sometimes narrowly excavated. Periostracum tan.

Operculum ovate, amber, reddish in nuclear region; nucleus eccentric; dorsal surface strongly frilled; outer margin smooth. Attachment scar thick almost all around; whorl edges slightly bulging.

Radula  $720 \times 114 \mu\text{m}$ , with 75 rows of teeth. Central tooth  $12 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 4–6 (often fused dorsally); central cusp narrow, daggerlike; basal cusps small, weakly developed. Basal tongue V-shaped, longer than lateral margins, basal sockets shallow. Lateral margins very narrow, strongly flared. Lateral tooth formula 5-1-6(7); neck weakly flexed; outer wing 290% of cutting edge length. Inner marginal teeth with 27–29 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 23–30 cusps; cutting edge occupying 22% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber, stomach caecum very small.

Cephalic tentacles light to medium brown. Snout, foot medium to dark brown. Opercular lobe medium to dark along outer edge. Neck unpigmented to medium brown. Pallial roof, visceral coil uniformly dark brown. Penial filament darkly pigmented internally for most of length; pigment often extending onto distal penis.

Ctenidial filaments, 11, without pleats, ctenidium connected to pericardium by short efferent vessel. Osphradium medium-sized (40–50%), narrow, positioned slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping glandular oviduct, abutting or slightly overlapping prostate gland.

Ovary 0.75–1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber.

Distal female genitalia shown in Figure 34F. Albumen gland having very short pallial component. Capsule gland slightly longer, but narrower than albumen gland, sub-circular in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland proximally, broadening distally; longitudinal fold weakly developed. Genital aperture a terminal slit, slightly raised distally, having short anterior extension. Coiled oviduct a single circular to posterior-oblique loop. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, up to 50% of length posterior to gland. Bursal duct originating from anterior edge, slightly shorter to as long as bursa, medium width. Seminal receptacle small, pouchlike, overlapping anterior half of bursa, sometimes extending to edge of albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping both stomach chambers anteriorly. Prostate gland bean-shaped, pallial portion very short, ovate in section. Proximal pallial vas deferens having U-shaped bend (toward ctenidium). Penis (Figure 34G) small, bladelikey; base near square, folded along inner edge; filament poorly distinguished from base, but apparently long, slightly narrower than base, tapering to rounded tip, longitudinal; lobe and glands absent. Penial duct straight, very close to outer edge.

**Type locality:** Spring, Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW  $\frac{1}{4}$  section 5. Holotype, USNM 873196 (Figure 19L), collected by J. J. Landye, 1 September 1980; paratypes, USNM 860682. The type locality is a small rheocrene adjacent to an old ranch house.

**Remarks:** This species is contrasted with *P. sulcata* above. The distribution of this snail is shown in Figure 51.

**Material examined:** NEVADA. *White Pine County:* Springs, Steptoe Ranch, USNM 860682, USNM 873196, USNM 892015.—Springs, ca. 1.6 km north-northwest of Steptoe Ranch, Steptoe Valley, T. 19 N, R. 63 E, NW  $\frac{1}{4}$  section 5, USNM 873195.

*Pyrgulopsis neritella* Hershler, sp. nov.

Neritiform Steptoe Ranch pyrg

(Figures 7L, 11G, 20A, 35A, B)

**Etymology:** From *nerita* (Latin), sea-snail (dim.); referring to the small, neritiform shell of this species.

**Diagnosis:** Small; with apically eroded neritiform shell. Penis small, filament long, lobe absent. Penial ornament a large Dg1.

**Description:** Shell (Figures 7L, 11G) neritiform, apex invariably eroded, width/height, 77–100%; height, 1.1–1.7 mm; width, 1.0–1.5 mm; whorls, about 3.5. Protoconch (Figure 11G) 1.25 whorls, diameter 0.27 mm;

strongly wrinkled, although sculpture weakening near teleoconch border. Teleoconch whorls moderately convex, strongly shouldered, usually bearing well developed sub-sutural cord or welt. Aperture broadly ovate, angled above, broadly adnate, sometimes having adapical portion loosened from body whorl. Inner lip thin, having broad columellar shelf (covering umbilical region). Outer lip thin, strongly prosocline, without sinuation. Umbilicus absent or narrowly rimate; umbilical region sometimes narrowly excavated. Periostracum light brown.

Operculum ovate, reddish; nucleus highly eccentric; dorsal surface smooth. Attachment scar thick all around.

Radula  $530 \times 80 \mu\text{m}$ , with 80 rows of teeth. Central tooth  $13 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 2–4 (most of cusp row completely fused dorsally); central cusp broad, having bifurcate or jagged edge; basal cusps absent, although region occasionally having very slight thickenings. Basal tongue V-shaped, longer than lateral margins, basal sockets shallow. Lateral margins very narrow. Lateral tooth formula 4-1-4(5); neck weakly flexed; outer wing 310% of cutting edge length. Inner marginal teeth with 26–30 cusps; cutting edge occupying 32% of length of tooth. Outer marginal teeth with 28–32 cusps; cutting edge occupying 21% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout, foot medium to dark brown. Opercular lobe dark along inner edge, sometimes all around. Neck unpigmented to medium brown. Pallial roof, visceral coil uniformly dark brown. Penial filament darkly pigmented internally; pigment often extending into proximal portion of base.

Ctenidium narrow; filaments, 12, without pleats, slightly overlapping pericardium posteriorly. Osphradium small, narrowly ovate, positioned slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 35A. Albumen gland without a pallial component. Capsule gland slightly longer but narrower than albumen gland, sub-circular in section, without anterior extension; rectal furrow well developed. Ventral channel narrowly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal pore borne on weak papilla extending distally to capsule gland. Coiled oviduct a single tight circular or posterior-oblique loop, sometimes kinked at mid-length. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix slightly shorter and narrower than albumen gland, broadly ovate, longitudinal, 50% of length posterior to gland. Bursal duct originating from

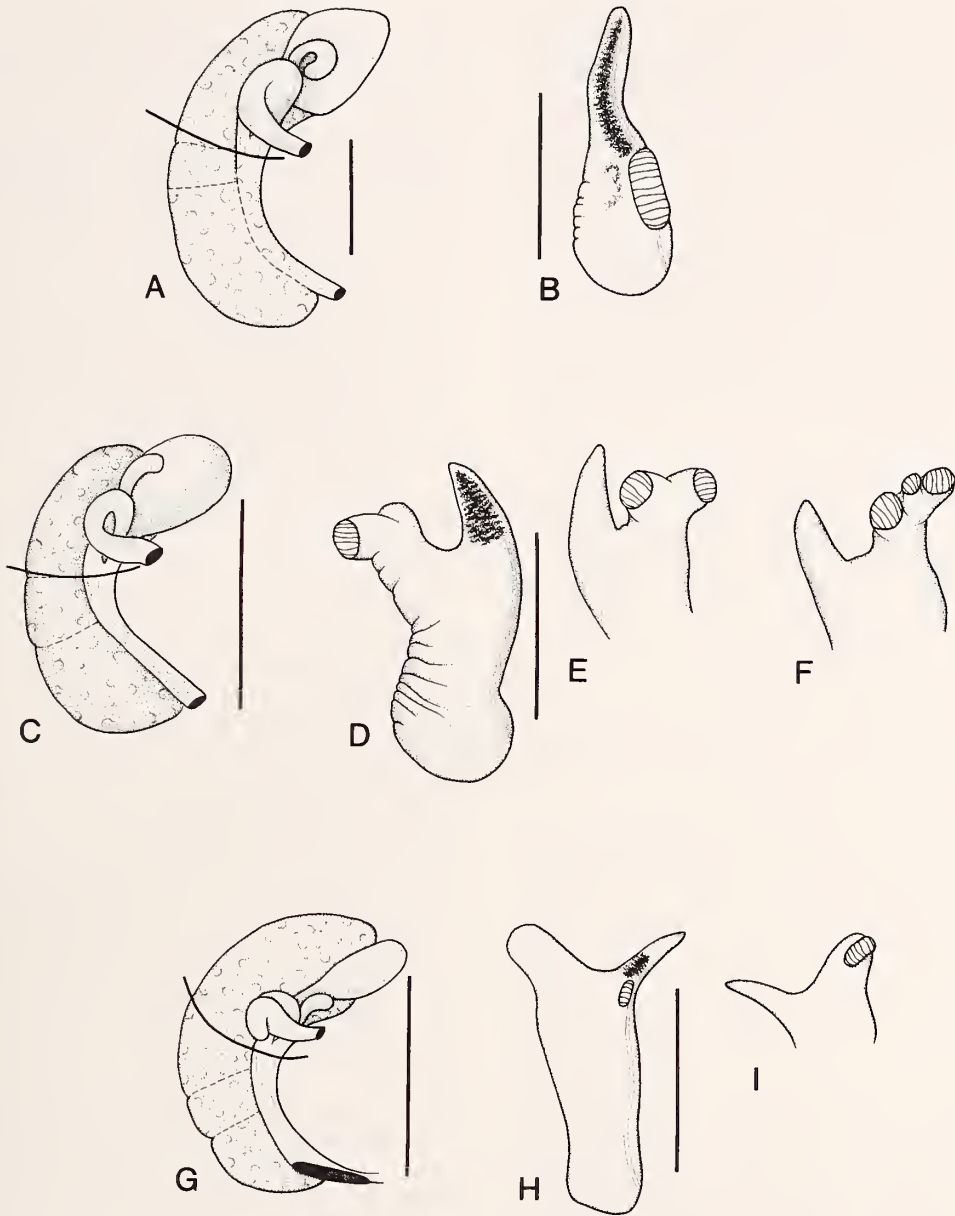


Figure 35

Genitalia of *Pyrgulopsis* species (A, B, *P. neritella*, USNM 860684; C–F, *P. landyei*, USNM 860685; G–I, *P. serrata*, USNM 860719). A, B. Bars = 0.25 mm. C–I. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. neritella* as ventral ornament absent).

anterior edge at mid-line, short, medium width. Seminal receptacle small, narrow, often coiled, overlapping anterior portion of bursa.

Testis 1.0 whorl, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland elongate bean-shaped, pallial portion large (50%), ovate in section. Proximal pallial vas deferens

straight or weakly bent. Penis (Figure 35B) small; base near square, poorly distinguished from filament, inner edge weakly folded; filament as long as and almost as wide as base, weakly tapered, longitudinal; lobe absent. Dg1, large, broad, sometimes slightly raised, borne along outer edge just proximal to filament. Penial duct straight, near outer edge.

**Type locality:** Springs, north of Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW ¼ section 5. Holotype, USNM 883932 (Figure 20A), collected by R. Hershler and P. Hovingh, 9 May 1995; paratypes, USNM 860684. The type locality is a series of thermal (23°C.) rheocrenes whose outflows enter an impoundment on a privately owned ranch. This site also harbors an undescribed species of *Tryonia*.

**Remarks:** This species is distinguished from other taxa found in southeast Steptoe Valley by its neritiform shell, pattern of penial ornamentation (consisting solely of a prominent Dg1), and distally extended and weakly papillate capsule gland opening. The distribution of this species is shown in Figure 51.

**Material examined:** NEVADA. *White Pine County:* Spring, north of Steptoe Ranch, USNM 860684, USNM 873194, USNM 883932.—Springs, just north of above, Steptoe Valley, T. 19 N, R. 63 E, SW ¼ section 5, USNM 883936.

*Pyrgulopsis landyei* Hershler, sp. nov.

Landyes pyrg

(Figures 8A, 20B, 35C–F)

**Etymology:** Named after J. Jerry Landye, in recognition of his long-term efforts to document and conserve aquatic mollusks in the western United States.

**Diagnosis:** Small, with broadly conical shell. Penis large, filament medium and lobe length. Penial ornament a large, fragmented terminal gland.

**Description:** Shell (Figures 8A, 20B) broadly conical, but apex invariably eroded, yielding a globular appearance, width/height, 83–98%; height, 1.3–1.7 mm; width, 1.3–1.7 mm; whorls, 3.0–4.25. Protoconch 1.25 whorls, diameter 0.27 mm, initial 0.75 whorl coarsely wrinkled, remaining portion finely wrinkled. Teleoconch whorls highly convex, shoulders well developed. Aperture broadly ovate, usually broadly adnate, rarely slightly disjunct. Inner lip thin, columellar shelf medium width. Outer lip thin, strongly prosocline, without sinuation. Umbilicus anomphalous or narrowly rimate; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum ovate, reddish; nucleus eccentric; dorsal surface frilled. Attachment scar thick all around; whorl edges sometimes slightly bulging.

Radula 550 × 80 µm, with 68 rows of teeth. Central tooth 15 µm wide, with highly indented dorsal edge; lateral cusps, 2–4 (cusp edge strongly fused dorsally); central cusp broad, triangular; basal cusps absent, although sometimes a weak swelling present. Basal tongue V-shaped, longer than lateral angles, basal sockets shallow. Lateral margins narrow, strongly flared. Lateral tooth formula 4(5)-1-3(4, 5); neck weakly flexed; outer wing 250% of cutting edge length. Inner marginal teeth with 25–27 cusps; cutting

edge occupying 29% of length of tooth. Outer marginal teeth with 27–32 cusps; cutting edge occupying 22% of length of tooth. Stomach longer than style sac; stomach chambers equal-sized; stomach caecum small.

Cephalic tentacles medium to dark brown. Snout, foot dark brown. Opercular lobe dark along inner edge, sometimes all around. Neck medium grey-brown. Pallial roof, visceral coil uniform dark brown to black. Penial filament darkly pigmented along most of length; black granules also scattered on base.

Ctenidial filaments, 13, without pleats, ctenidium connected to pericardium by short efferent vessel. Oosphradium small, narrow, positioned centrally or slightly posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 35C. Albumen gland with extremely short or no pallial component. Capsule gland slightly longer and as wide as albumen gland, sub-globose in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit mounted on a weak papilla, without anterior extension. Coiled oviduct a posterior-oblique loop sometimes preceded by posterior-oblique twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length, slightly narrower to as wide as albumen gland, broadly ovate, longitudinal, with 50–75% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, short, medium width, proximal portion often looping. Seminal receptacle small, pouch-like, often coiled, overlapping anterior portion of bursa.

Testis 1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion medium, ovate in section. Proximal pallial vas having well-developed loop. Penis (Figure 35D–F) large; base rectangular, inner edge folded; filament medium length and width, tapering to point, longitudinal; lobe as long as filament, clublike, often distally bifurcate, slightly oblique. Terminal gland large, composed of two circular units borne on edges of distally bifurcate lobe; one to two smaller, but similarly circular units sometimes present, positioned between main glands. (Lobe rarely simple, with single terminal gland.) Occasional specimens having dotlike or narrow, distal Dg2. Penial duct straight, very close to outer edge.

**Type locality:** Spring, ca. 1.6 km north-northwest of Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, NW ¼ section 5 (Figure 51). Holotype, USNM 892014 (Figure 20B), collected by J. Landye, 21 November 1995; paratypes, USNM 860685. The type locality is a small rheocrene whose headspring is protected by an old fence.

**Remarks:** This species differs from others found in southeast Steptoe Valley in having a well-developed penial lobe and penial ornament consisting of a bifurcate terminal gland.

**Material examined:** NEVADA. *White Pine County:* Spring, ca. 1.6 km north-northwest of Steptoe Ranch, USNM 860685, USNM 892012, USNM 892014.

*Pyrgulopsis serrata* Hershler, sp. nov.

Northern Steptoe pyrg

(Figures 8B, 15D–F, 20C–E, 35G–J)

**Etymology:** From *serratus* (Latin), toothed like a saw; referring to the numerous cusps on the radular teeth of this species.

**Diagnosis:** Medium-sized, with ovate- to narrow-conic shell. Penis medium-sized, filament and lobe medium length. Penial ornament of small terminal and penial glands.

**Description:** Shell (Figures 8B, 20C–E) ovate- to narrow-conic (almost turritiform), width/height, 56–87%; height, 2.0–4.1 mm; width, 1.5–2.6 mm; whorls, 4.0–5.25. Protoconch 1.3 whorls, diameter 0.33 mm, initial 0.75 whorl finely wrinkled (stronger along inner edge), later portion near smooth. Teleoconch whorls moderately to highly convex, shouldered. Aperture ovate, narrowly adnate or slightly disjunct. Inner lip sometimes thick, without columellar shelf. Outer lip thin or thick, prosocline, without sinuation. Umbilicus rimate to perforate; umbilical region often narrowly excavated. Periostracum tan.

Operculum ovate, amber, reddish in nuclear region; nucleus eccentric; dorsal surface frilled; outer margin sometimes having weak rim. Attachment scar slightly thickened between nucleus and inner edge, sometimes similarly thick all around.

Radula (Figure 15D–F)  $860 \times 148 \mu\text{m}$ , with 67 rows of teeth. Central tooth  $18 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 7–9; central cusp medium width, daggerlike; basal cusps large. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-4(6); neck weakly flexed; outer wing 215% of cutting edge length. Inner marginal teeth with 29–33 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 31–33 cusps; cutting edge occupying 25% of length of tooth. Stomach and style sac equal in length; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented (except for short stripe just distal to eyes) to medium grey. Snout, foot unpigmented to medium grey. Opercular lobe dark along inner edge, sometimes pigmented all around. Neck unpigmented or light grey. Pallial roof, visceral coil uniform black. Proximal portion to entire penial filament darkly pigmented internally.

Ctenidium narrow; filaments, 14, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, positioned slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber anteriorly. Distal female genitalia shown in Figure 35G. Albumen gland having 33% of length in pallial cavity. Capsule gland shorter and narrower than albumen gland, sub-circular in section; rectal furrow very weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit with short anterior extension. Coiled oviduct of two small, overlapping, posterior oblique loops. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix short, narrow, narrowly ovate, positioned near ventral edge of albumen gland, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, slightly shorter to as long as bursa, medium width. Seminal receptacle small, narrow, overlapping or ventral to anteriormost portion of bursa or proximal bursal duct.

Testis 1.0–1.25 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and small part of anterior stomach chamber. Prostate gland very small, ovate, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having well-developed bend (often slightly reflexed). Penis (Figure 35H, I) medium-sized; base rectangular, lacking folds; filament slightly shorter than base, tapering to point, medium width, slightly oblique; lobe slightly longer than filament, knoblike, slightly oblique. Terminal gland small, narrow, ventral, nearly longitudinal. Penial gland small, rarely medium-sized, sometimes minute or absent in stunted penes, slightly narrower to as wide as filament, sometimes raised, positioned near base of filament (sometimes slightly overlapping base). Penial duct straight, near outer edge.

**Type locality:** Indian Ranch Spring, Steptoe Valley, White Pine County, Nevada, T. 26 N, R. 63 E, NE  $\frac{1}{4}$  section 20. Holotype, USNM 874314 (Figure 20C), collected by R. Hershler, 4 August 1991; paratypes, USNM 860719. The type locality is a shallow, but broad (>30 m) rheocene coursing down a forested mountain slope.

**Remarks:** Among the group of species having penial ornament solely consisting of a terminal gland and small penial gland, *P. serrata* most closely resembles *P. anatina*, from Railroad Valley. *Pyrgulopsis serrata* differs from *P. anatina* in having a longitudinal (not transverse) terminal gland and smaller penial gland. The distribution of *P. serrata* is shown in Figure 51.

**Material examined:** NEVADA. *Elko County:* Twin Springs, Steptoe Valley, T. 29 N, R. 63 E, NE  $\frac{1}{4}$  section

35, USNM 874318.—Springs, south of Currie, Steptoe Valley, T. 27 N, R. 64 E, NW  $\frac{1}{4}$  section 10, USNM 874312. *White Pine County*: Indian Ranch Spring, USNM 860719, USNM 874314.—Indian Creek, Steptoe Valley, T. 26 N, R. 64 E, section 20, USNM 858018.

*Pyrgulopsis cruciglans* Hershler, sp. nov.

Transverse gland pyrg

(Figures 8C, 20F–H, 36A, B)

**Etymology:** From *crux* (Latin), cross; and *glans*, acorn or gland; referring to the prominent transverse dorsal gland (Dg1) on the penis of this species.

**Diagnosis:** Small to medium-sized, with ovate- to narrow-conic shell. Penis medium-sized, filament medium length, lobe long. Penial ornament a large Dg1.

**Description:** Shell (Figures 8C, 20F–H) ovate- to narrow-conic, width/height, 71–85%; height, 1.6–2.7 mm; width, 1.3–2.1 mm; whorls, 4.0–4.75. Protoconch 1.25 whorls, diameter 0.29 mm, surface smooth except for weak wrinkling around edges of apex. Teleoconch whorls moderately convex, weakly shouldered. Aperture ovate, narrowly adnate to slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus rimate or perforate. Periostracum tan-brown, often covered with thick brown deposits.

Operculum ovate, amber; nucleus eccentric; dorsal surface frilled; outer margin sometimes having weak rim. Attachment scar thick, sometimes greatly so, along most of perimeter (except for portion of outer edge).

Radula  $820 \times 130 \mu\text{m}$ , with 65 rows of teeth. Central tooth  $17 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 6–7; central cusp narrow, daggerlike; basal cusps medium-sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-4(5); neck weakly flexed; outer wing 230% of cutting edge length. Inner marginal teeth with 24–27 cusps; cutting edge occupying 30% of length of tooth. Outer marginal teeth with 30–32 cusps; cutting edge occupying 25% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to light grey. Snout light to medium grey-brown. Foot unpigmented to light grey. Opercular lobe light grey to black along inner edge. Neck light grey. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally for most of length; lobe, especially distal portion, containing scattered black granules.

Ctenidial filaments, 15, weakly pleated; ctenidium overlapping pericardium posteriorly. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5–0.75 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 36A. Albumen gland having very short pallial component. Capsule gland slightly shorter and narrower than albumen gland, ovate in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique to horizontal loop preceded by well-developed twist or small coil. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, broadly-ovate to sub-globular, longitudinal, with 50–67% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% to almost as long as bursa, medium width. Seminal receptacle small, pouchlike to narrow, overlapping anterior portion of bursa.

Testis 1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior and small portion of anterior stomach chambers. Prostate gland broadly ovate, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having well-developed, reflexed bend. Penis (Figure 36B) medium-sized; base nearly square, weakly folded along inner edge; filament slightly shorter than base, narrow, tapering to pointed tip, longitudinal; lobe as long or longer than base; tapering to rounded tip, sometimes greatly narrowed distally, longitudinal. Dg1 large, rarely divided into two units; borne on fleshy pedicel, transverse, positioned slightly proximal to filament. Weak, dotlike Dg3 seen in one specimen. Ventral surface sometimes bearing central swelling, but lacking gland(s). Penial duct straight, near outer edge.

**Type locality:** Flat Spring, Steptoe Valley, White Pine County, Nevada, T. 25 N, R. 66 E, SE  $\frac{1}{4}$  section 2, collected by R. Hershler, 5 August 1991. Holotype, USNM 874285 (Figure 20F), collected by R. Hershler, 5 August 1991; paratypes, USNM 860709. The type locality is a shallow, broad (13 m) rheocene which has been dug out and impounded.

**Remarks:** This species is distinguished from other congeners by its unique penial ornament, which consists solely of a very large, transverse Dg1 borne on a prominent swelling. *Pyrgulopsis cruciglans* also has an unusually broad oviduct coil. The distribution of this species is shown in Figure 52.

**Material examined:** NEVADA. *White Pine County*: Flat Spring, USNM 860709, USNM 874285. *Elko County*: Boone Spring, Antelope Valley, T. 27 N, R. 67 E, SE  $\frac{1}{4}$  section 29, USNM 874327.—Dolly Varden Spring, Antelope Valley, T. 28 N, R. 67 E, NW  $\frac{1}{4}$  section 9, USNM 874335.—Ferguson Springs, Great Salt Lake Basin, T. 30 N, R. 69 E, NE  $\frac{1}{4}$  section 33, USNM 874331.



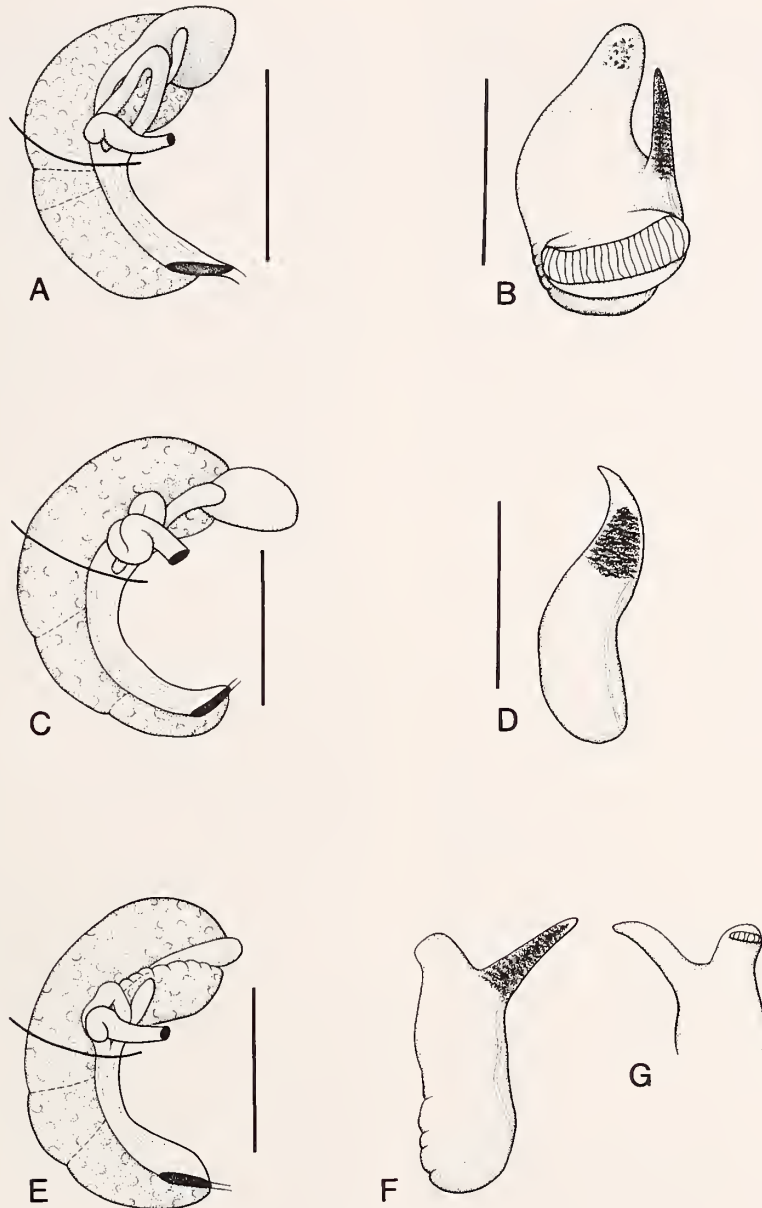


Figure 36

Genitalia of *Pyrgulopsis* species (A, B, *P. cruciglans*, USNM 860709; C, D, *P. dixensis*, USNM 860688; E-G, *P. aurata*, USNM 860696). A, B. Bars = 0.5 mm. C, D. Bars = 0.25 mm. E-G. Bar = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. dixensis* and *P. aurata* as penial ornament absent on the ventral surface in these species).

*Pyrgulopsis dixensis* Hershler, sp. nov.

Dixie Valley pyrg

(Figures 8D, 13C, 20I, J, 36C, D)

**Etymology:** Referring to endemism of this species in Dixie Valley, Nevada.

**Diagnosis:** Small, with elongate-conic shell. Penis small,

bladelike; filament medium length, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 8D, 20I, J) elongate-conic, width/height, 48–56%; height, 1.6–2.0 mm; width, 0.8–1.0 mm; whorls, 5.0–5.75. Protoconch 1.25 whorls, diameter 0.28 mm, weakly wrinkled at apex, otherwise smooth. Early teleoconch whorls highly convex, later whorls near flat to

medium convexity, often strongly angled below periphery; shoulder often well developed, but narrow; body whorl often slightly disjunct behind the aperture. Aperture ovate, angled above, broadly adnate or slightly disjunct. Inner lip thin, without columellar shelf. Outer lip thin, prosocline, weakly sinuate. Shell anomphalous or with narrowly rimate umbilicus. Periostracum tan.

Operculum (Figure 13C) ovate, amber; nucleus eccentric; dorsal surface very strongly frilled; outer margin sometimes having weak rim. Attachment scar slightly thickened between nucleus and inner edge, whorl edges strongly bulging.

Radula  $335 \times 60 \mu\text{m}$ , with 52 rows of teeth. Central tooth  $13 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp narrow, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck medium flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 20–24 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 23–28 cusps; cutting edge occupying 25% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or light grey proximally. Snout unpigmented to medium grey-brown. Foot unpigmented or having scattered grey pigment. Opercular lobe medium grey along inner edge, sometimes along sides, unpigmented or diffuse light grey elsewhere. Neck having scattered grey granules to medium grey. Pallial roof and visceral coil medium grey-black, usually lighter on former; gonads often uniform black. Proximal portion of penial filament and distal portion of base darkly pigmented internally.

Ctenidial filaments, 15, without pleats; ctenidium connected to pericardium by medium length efferent vein. Osphradium small, narrow, positioned centrally to slightly posterior to middle of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum straight; broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, abutting posterior edge of stomach. Distal female genitalia shown in Figure 36C. Albumen gland having medium-large (33–45%) pallial component. Capsule gland shorter, narrower than albumen gland, narrowly ovate in section, rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two small, overlapping posterior-oblique loops. Oviduct and bursal duct joining at pallial wall. Bursa copulatrix medium length and width, ovate to weakly pyriform, longitudinal, with 50–80% of length posterior to gland. Bursal duct originating from anterior edge at or slightly lateral to mid-line, slightly shorter to slightly longer than bursa, medium width. Seminal receptacle narrow pouchlike, sometimes weakly folded, overlapping anterior portion of bursa.

Testis 1.5 whorls, filling 50% of digestive gland behind

stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland small, elongate bean-shaped, pallial portion medium-large (40–50%), narrowly ovate in section. Proximal pallial vas deferens straight. Penis (Figure 36D) small, bladelike; base rectangular, smooth or weakly folded; filament poorly distinguished from base, but apparently medium length and width, tapering to point, longitudinal; lobe absent, distal portion of base gently tapering to filament. Penis lacking glands. Penial duct straight, very close to outer edge.

**Type locality:** Springs, west-southwest of Hot Springs, Dixie Valley, Pershing County, Nevada, T. 25 N, R. 39 E, SE  $\frac{1}{4}$  section 18 (Figure 52). Holotype, USNM 874391 (Figure 20I), collected by D. W. Sada, 8 September 1991; paratypes, USNM 860688. The type locality is the southernmost spring in a complex of mineralized (1090 micromhos/cm) helocrenes.

**Remarks:** Among the group of simple-pened species of *Pyrgulopsis*, this species and *P. augustae* (described below), from nearby Antelope Valley, share a tall shell, weak protoconch microsculpture, short penial filament, and relatively complex coiled oviduct. *Pyrgulopsis dixensis* differs from *P. augustae* in its smaller, narrower shell and much weaker frilling of operculum whorls.

**Material examined:** NEVADA. *Pershing County*: Springs, west-southwest of Hot Springs, USNM 860688, USNM 874391.

*Pyrgulopsis aurata* Hershler, sp. nov.

Pleasant Valley pyrg

(Figures 8E, 20K, L, 36E–G)

**Etymology:** From *auratus* (Latin), golden; referring to endemism of this species in the Goldbanks Hills, Nevada.

**Diagnosis:** Medium-sized, with ovate-conic shell. Penis medium-sized; filament medium length, lobe short. Penial ornament a small terminal gland.

**Description:** Shell (Figures 8E, 20K, L) ovate-conic, width/height, 75–83%; height, 2.5–3.0 mm; width, 2.0–2.4 mm; whorls, 4.25–4.75. Protoconch 1.25 whorls, diameter 0.33 mm, weakly wrinkled along edges at apex, otherwise smooth. Teleoconch whorls medium convexity, sutures often impressed, usually shouldered, body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thick, sometimes having narrow columellar shelf. Outer lip thin, orthocline, weakly sinuate. Umbilicus rimate-perforate. Periostracum tan.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric. Attachment scar slightly thickened between nucleus and inner edge and along inner edge.

Radula  $730 \times 110 \mu\text{m}$ , with 60 rows of teeth. Central tooth  $24 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 4–5; central cusp narrow, daggerlike; basal

cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3, 4)-1-3(4); neck medium flexed; outer wing 180% of cutting edge length. Inner marginal teeth with 19–20 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 23–33 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light grey or black proximally. Snout unpigmented to medium grey. Foot unpigmented to light grey. Opercular lobe usually black all around, sometimes unpigmented except for black streak along inner edge. Neck unpigmented, except for scattered black granules, to medium grey. Pallial roof, visceral coil often uniformly black, sometimes having lighter pigment on genital ducts. Penial filament darkly pigmented internally.

Ctenidial filaments, 18, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned centrally or slightly posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 36E. Albumen gland having short pallial component. Capsule gland considerably shorter, as wide or slightly narrower than albumen gland sub-circular in section rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop (sometimes kinked at mid-line) usually preceded by well-developed posterior twist. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix much shorter, narrow, ovate, longitudinal, sometimes overlapped by gland along ventral edge, 25% or less of length posterior to gland. Bursal duct originating from anterior edge at mid-line, usually poorly distinguished from bursa (which gently tapers anteriorly), slightly longer to twice as long as bursa, narrow-medium width, usually overlapped by albumen gland for 50% of length (distally). Seminal receptacle small, narrow pouchlike, positioned well anterior to bursa copulatrix.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland small, bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens with well-developed bend; duct broad. Penis (Figure 36F, G) medium-sized; base elongate-rectangular, inner edge weakly folded; filament a little shorter than base, medium width, tapering to point; lobe shorter than filament, knob-like, longitudinal. Terminal gland small, narrow, transverse, largely or entirely on ventral surface. Penial duct straight, near edge.

**Type locality:** Coyote Spring, Pleasant Valley, Pershing

County, Nevada, T. 30 N, R. 39 E, SE ¼ section 30 (Figure 52). Holotype, USNM 874393 (Figure 20K), collected by D. W. Sada, 7 September 1991; paratypes, USNM 860696. The type locality is a small rheocene severely impacted by cattle.

**Remarks:** Among the large group of species having penial ornament solely consisting of a terminal gland, this species closely resembles *P. bryantwalkeri* Hershler, 1994, locally endemic in upper Humboldt basin, in shape of shell and configuration of distal female genitalia. *Pyrgulopsis aurata* differs in having a nearly smooth protoconch, stronger development of terminal gland (often absent in *P. bryantwalkeri*), narrower bursa copulatrix, and more anteriorly positioned seminal receptacle.

**Material examined:** NEVADA. *Pershing County:* Coyote Spring, USNM 860696, USNM 874393.

### Species from the Lahontan Basin

#### *Pyrgulopsis gibba* Hershler, 1995

“Undescribed form of *Fontelicella*” Taylor, 1985:318 [in part; Walker River drainage].

*Pyrgulopsis owensensis* Hershler, 1989, Hershler & Pratt, 1990:287 [Walker River drainage; not Hershler, 1989].

“Undescribed . . . closely similar [to *P. owensensis*] species” Hershler, 1994:57.

*Pyrgulopsis gibba* Hershler, 1995:354, 357, 358, figs. 5C, 10–12.

**Diagnosis:** Medium-sized (rarely small), with ovate- to narrow-conic shell. Penis large; filament medium length, lobe long. Penial ornament a large terminal gland, small Dg3 (sometimes absent), and large ventral gland.

**Type locality:** Springs west of Fee Reservoir, Surprise Valley, Modoc County, California, T. 46 N, R. 17 E, NE ¼ section 20 (Hershler, 1995:fig. 4C).

**Remarks:** The distribution of this snail, previously known from Surprise and Duck Lake Valleys in northeastern California, is herein extended into western Nevada to include much of the Lahontan Basin and isolated drainages in the central (Big Smokey, Grass, Smith Creek Valleys) and northwest (Long Valley) parts of the state (Figure 54). The range of this species closely abuts that of widespread *P. kolobensis* and they co-occur in one basin (Crescent Valley), although they are not found in the same springs.

Morphology of this snail is rather uniform throughout its broad range, although populations vary somewhat in size, shell shape, and penial ornament. The terminal gland on the penis may be weakly or strongly fragmented, and in the latter instance is usually accompanied by distal bifurcation of the penial lobe. Development of the ventral gland and Dg3 also varies. Material of this species from the East Walker River drainage was previously treated by the author as disjunct *P. owensensis* (which otherwise is

restricted to the Owens River drainage). Although these species can be confused owing to the general similarity in penial morphology, *P. gibba* is distinguished by various features, including a larger terminal gland on the penis, absence of Dg1, larger seminal receptacle and bursa copulatrix, and pigmented coiled oviduct.

**Material examined:** CALIFORNIA. *Mono County:* Spring, below Bridgeport Reservoir, East Fork Walker River, T. 6 N, R. 25 E, NW ¼ section 23, USNM 860452. NEVADA. *Elko County:* Spring, Antelope Creek, Humboldt River drainage, T. 37 N, R. 49 E, NE ¼ section 8, USNM 874375, USNM 883987.—Springs, Antelope Creek (upstream from above), Humboldt River drainage, T. 37 N, R. 49 E, SE ¼ section 5, USNM 883988.—Spring, Squaw Creek, Humboldt River drainage, T. 38 N, R. 49 E, SE ¼ section 34, USNM 883986.—Buffalo Springs, Squaw Valley, T. 40 N, R. 47 E, center section 32, USNM 883447. *Eureka County:* Willy Billy Spring, Humboldt River drainage, T. 32 N, R. 51 E, NE ¼ section 32, USNM 874714.—Rattlesnake Spring, Humboldt River drainage, T. 31 N, R. 50 E, NE ¼ section 2, USNM 874812, USNM 883425.—Springs, Pine Creek, Humboldt River drainage (Figure 4F), T. 31 N, R. 52 E, NE ¼ section 7, USNM 858277, USNM 874284.—Willow Spring, Horse Creek Valley, T. 26 N, R. 49 E, NW ¼ section 20, USNM 874310.—Stream, Corral Canyon, Crescent Valley, T. 29 N, R. 47 E, SW ¼ section 32, USNM 874322.—Cold Springs (north), Crescent Valley, T. 31 N, R. 48 E, NE ¼ section 36, USNM 874718. *Humboldt County:* Buck Springs, Black Rock Desert, T. 37 N, R. 24 E, SE ¼ section 23, USNM 874298.—Spring, Tollhouse Canyon, Soldier Meadow drainage, T. 41 N, R. 25 E, section 10, USNM 873201, USNM 873228, USNM 873235.—Buckbrush Springs, Black Rock Desert, T. 38 N, R. 30 E, NE ¼ section 9, USNM 874202, USNM 874894, USNM 883893.—Spring, Bliss Canyon, Black Rock Desert, T. 39 N, R. 31 E, SW ¼ section 6, USNM 874201, USNM 874907.—Springs, near mouth of Jackson Canyon, Black Rock Desert, T. 40 N, R. 31 E, NW ¼ section 28, USNM 874200, USNM 874892.—Springs, Jackson Canyon, Black Rock Desert, T. 40 N, R. 31 E, NE ¼ section 28, USNM 874203, USNM 874906.—Spring, Pueblo Mountains, Alberson Basin, T. 47 N, R. 29 E, NW ¼ section 1, USNM 874214, USNM 874908.—Spring, 0.4 km south of above, Pueblo Mountains, Alberson Basin, T. 47 N, R. 29 E, NW ¼ section 1, USNM 874900.—Craine Creek, Bog Hot Valley, T. 42 N, R. 27 E, NW ¼ section 2, USNM 883924.—Spring, Pearl Canyon, Quinn River Valley, T. 42 N, R. 27 E, center section 25, USNM 883898.—Hillside Spring, Alta Creek Basin, Quinn River Valley, T. 45 N, R. 30 E, NE ¼ section 7, USNM 873429.—Spring, Canyon Creek, Quinn River Valley, T. 45 N, R. 38 E, SW ¼ section 18, USNM 883994.—Spring, 1.6 km northwest of Dyke Hot Springs, Quinn River Valley, T. 42 N, R. 30 E, NW ¼

section 25, USNM 874216, USNM 874743.—Spring, Bishop Canyon, Quinn River Valley, T. 42 N, R. 30 E, SW ¼ section 23, USNM 874210, USNM 874893.—Bonita Spring, Quinn River Valley, T. 37 N, R. 30 E, NE ¼ section 2, USNM 854687.—Trout Creek, Desert Valley, T. 39 N, R. 32 E, NE ¼ section 6, USNM 874217.—Spring, Rock Creek, Humboldt River drainage, T. 34 N, R. 40 E, SW ¼ section 6, USNM 874399.—Spring, Kelly Creek, Humboldt River drainage, T. 40 N, R. 44 E, SW ¼ section 33, USNM 854696.—Spring, Spring Creek, Little Humboldt River drainage, T. 41 N, R. 43 E, NE ¼ section 23, USNM 883922.—Layton Spring, South Fork Little Humboldt River, T. 41 N, R. 43 E, SE ¼ section 11, USNM 883897, USNM 883923. *Lander County:* Twin Spring, Grass Valley, T. 22 N, R. 47 E, SE ¼ section 12, USNM 874300.—Stream, Potato Canyon, Grass Valley, T. 23 N, R. 48 E, NE ¼ section 9, USNM 874329.—Spring, Fish Creek, Reese River Valley, T. 27 N, R. 42 E, center section 16, USNM 883849.—Spring, southwest of Bradley Spring, Reese River Valley, T. 22 N, R. 43 E, NE ¼ section 28, USNM 874400.—Twin Springs, Smith Creek Valley, T. 18 N, R. 39 E, NW ¼ section 27, USNM 874407. *Lyon County:* Spring, (lower) Dalzell Canyon, Smith Valley, T. 8 N, R. 25 E, NW ¼ section 5, USNM 860453, USNM 874394.—Spring, (upper) Dalzell Canyon, Smith Valley, T. 9 N, R. 24 E, SW ¼ section 24, USNM 873352, USNM 874398.—Spring, Nye Canyon, Smith Valley, T. 8 N, R. 25 E, NE ¼ section 9, USNM 883544. *Nye County:* Spring, Indian Creek, Reese River Valley, T. 11 N, R. 40 E, NW ¼ section 4, USNM 874379, USNM 874395.—Springs, RO Ranch, Big Smokey Valley, T. 13 N, R. 44 E, NE ¼ section 32, USNM 874405. *Pershing County:* Buffalo Springs, Buena Vista Valley, T. 27 N, R. 35 E, west ½ section 2, USNM 874752, USNM 883449.—Spring, 1.6 km west of Fitting, Buena Vista Valley, T. 29 N, R. 34 E, S ½ section 35, USNM 874747.—Spring, Spring Valley, T. 28 N, R. 34 E, NW ¼ section 3, USNM 874751, USNM 883482.—Dago Spring, Buena Vista Valley, T. 27 N, R. 37 E, NW ¼ section 16, USNM 874737.—Buena Vista Creek, Buena Vista Valley, T. 30 N, R. 34 E, NE ¼ section 28, USNM 883453.—Kitten Spring, Buena Vista Valley, T. 25 N, R. 36 E, NW ¼ section 10, USNM 874750.—Twin Springs, Buena Vista Valley, T. 27 N, R. 37 E, SW ¼ section 29, USNM 874748.—Porter Spring, Granite Springs Valley, T. 29 N, R. 28 E, NW ¼ section 5, USNM 883446.—Spring, 0.4 km east of Porter Spring, Granite Springs Valley, T. 29 N, R. 28 E, NE ¼ section 5, USNM 874749, USNM 883433.—Spring (pond outflow), Sheep Ranch Canyon, Grass Valley, T. 32 N, R. 39 E, NW ¼ section 16, USNM 874746.—Spring, Clearwater Creek, Grass Valley, T. 33 N, R. 38 E, SW ¼ section 13, USNM 874755, USNM 883440.—Spring, Sacramento Canyon, Humboldt River drainage, T. 29 N, R. 33 E, NE ¼ section 35, USNM 874742.—Spring, Pleasant Valley Ranch, Pleasant Valley, T. 27 N, R. 38 E, NE

¼ section 2, USNM 874389. *Washoe County*: Spring, Hog Gulch, Surprise Valley, T. 42 N, R. 18 E, SE ¼ section 10, USNM 883989.—North Spring, Surprise Valley, T. 42 N, R. 18 E, NW ¼ section 11, USNM 883992.—Small Spring, Surprise Valley, T. 41 N, R. 18 E, NW ¼ section 28, USNM 883990.—Spring, 3.2 km south of Mosquito Lake, Mosquito Valley, T. 45 N, R. 19 E, SE ¼ section 22, USNM 874204, USNM 874897.—Spring, west of Alkali Lake, Long Valley, T. 44 N, R. 19 E, NW ¼ section 32, USNM 874205.—Spring, Vya, Long Valley, T. 42 N, R. 19 E, SW ¼ section 4, USNM 874898.—Spring, 3.2 km northeast of Middle Lake, Long Valley, T. 45 N, R. 21 E, SW ¼ section 30, USNM 874895.—Spring, Wall Creek, 1.6 km above reservoir, Duck Flat drainage, T. 38 N, R. 19 E, SE ¼ section 12, USNM 874287, USNM 883926.—Spring, Wall Creek, 4.8 km above reservoir, Duck Flat drainage, T. 38 N, R. 20 E, NE ¼ section 6, USNM 874268, USNM 883925.—“Deep Hole Spring” (=“Big Hole Spring”), 14.4 km west-northwest of Gerlach, Smoke Creek Desert, T. 33 N, R. 22 E, NW ¼ section 27, USNM 873230, USNM 874272.—Spring, Red Mountain Creek, Hualapai Flat, T. 35 N, R. 22 E, SW ¼ section 15, USNM 874198, USNM 874905.—Spring, Red Mountain Creek, Hualapai Flat, T. 35 N, R. 22 E, SW ¼ section 14, USNM 874890. *OREGON*. *Lake County*: Foskett Spring, Coleman Valley, T. 40 S, R. 24 E, NW ¼ section 25, USNM 883545, USNM 892031.—Moss Spring, Chewaucan River drainage, T. 36 S, R. 19 E, SE ¼ section 5, USNM 883543.

*Pyrgulopsis wongi* Hershler, 1989

*Pyrgulopsis wongi* Hershler, 1989:196, figs. 41–47.

**Diagnosis:** Small to medium-sized, with globose to low-conical shell. Penis large; filament and lobe medium length. Penial ornament a large terminal gland, large penial gland, large, fused Dg1–2; medium-sized Dg3, two to five additional dorsal glands; and two medium-sized ventral glands.

**Type locality:** Spring, Birchim Canyon, Owens Valley, Inyo County, California, T. 6 S, R. 31 E, SE ¼ section 9.

**Remarks:** The range of this species, previously constituting the pluvial Owens River drainage and adjacent basins (Deep Springs, Fish Lake, and Huntoon Valleys), is herein extended to a portion of the eastern Lahontan Basin (upper portions of the Carson and East Walker River drainages), and a nearby, isolated drainage (Teels Marsh) (Figure 52). This snail does not exhibit marked variation in shell or anatomical features.

**Material examined:** CALIFORNIA. *Mono County*: Spring, Clark Canyon, East Walker River drainage, T. 4 N, R. 25 E, SE ¼ section 1, USNM 874191.—Spring, Clearwater Creek, East Walker River drainage, T. 4 N, R. 26 E, NW ¼ section 28, USNM 874193.—Spring, Rough

Creek, East Walker River drainage, T. 5 N, R. 27 E, SE ¼ section 7, USNM 874188. NEVADA. *Douglas County*: Doud Springs, Carson River drainage, T. 11 N, R. 21 E, SE ¼ section 20, USNM 874741. *Esmeralda County*: Spring, southwest of The Crossing, Fish Lake Valley, T. 1 S, R. 36 E, SW ¼ section 17, USNM 883983.—Spring, southwest of The Crossing, 75 m west of above, Fish Lake Valley, T. 1 S, R. 36 E, SW ¼ section 17, USNM 883982. *Mineral County*: Spring, Bodie Creek, East Walker River drainage, T. 6 N, R. 27 E, SE ¼ section 25, USNM 874404.—Jacks Spring, Teels Marsh drainage, T. 2 N, R. 31 E, NE ¼ section 2, USNM 874763, USNM 874880.

*Pyrgulopsis longiglans*, Hershler, sp. nov.

Western Lahontan pyrg

(Figures 8F, 20M–P, 37A–C)

**Etymology:** From *glans* (Latin), gland; and *longus*, long; referring to the elongate penial gland characterizing this species.

**Diagnosis:** Small to medium-sized, with sub-globose to ovate-conic shell. Penis large; filament and lobe medium length. Penial ornament a large terminal gland, large penial gland, small Dg1, small Dg2, and large ventral gland (sometimes reduced or absent).

**Description:** Shell (Figures 8F, 20M–P) sub-globose to ovate-conic, width/height, 67–88%; height, 1.4–2.6 mm; width, 1.1–1.9 mm; whorls, 3.75–4.5. Protoconch 1.25–1.3 whorls, diameter 0.29 mm, initial 0.75 whorl weakly wrinkled along inner edge, otherwise smooth. Teleoconch whorls medium convexity; shoulders well developed, sutural shelf often broad. Aperture ovate, adnate or slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, orthocone-slightly prosocline, without sinuation. Umbilicus rimate-shallowly perforate. Periostracum tan.

Operculum ovate, reddish; nucleus eccentric; dorsal surface smooth or weakly frilled. Attachment scar slightly thickened between nucleus and inner edge, and along outer edge.

Radula 1.05 mm × 140 μm, with 63 rows of teeth. Central tooth 23 μm wide, with medium indented dorsal edge; lateral cusps, 3–5; central cusp medium width, daggerlike; basal cusps medium-sized. Basal process V-shaped, basal sockets deep. Lateral tooth formula 2(3)-1-3; neck weakly flexed; outer wing 175% of cutting edge length. Inner marginal teeth with 18–22 cusps (basal cusp enlarged); cutting edge occupying 36% of length of tooth. Outer marginal teeth with 28–32 cusps; cutting edge occupying 27% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles having small black patch of internal

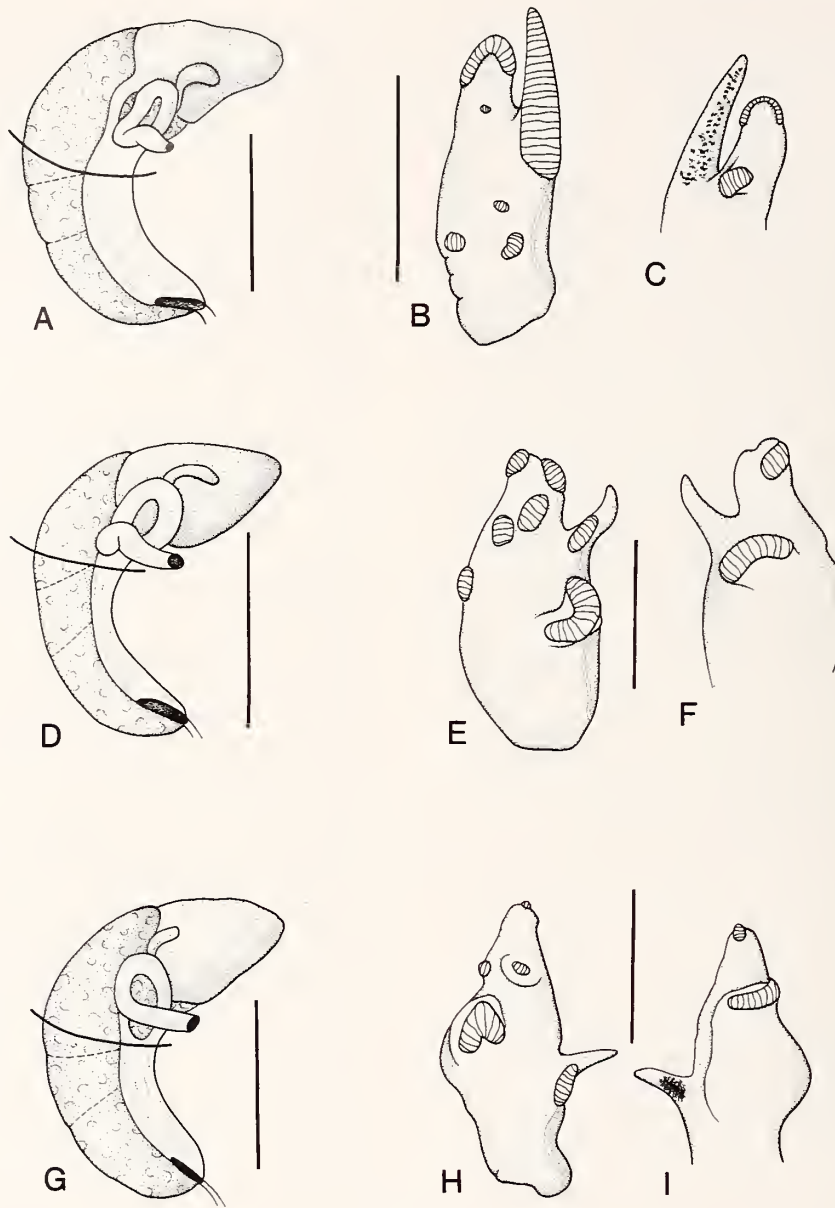


Figure 37

Genitalia of *Pyrgulopsis* species (A, *P. longiglans*, USNM 860701; B, C, *P. longiglans*, USNM 874745; D-F, *P. militaris*, USNM 860704; G-I, *P. umbilicata*, USNM 860705). A. Bar = 0.5 mm. B, C. Bar = 1.0 mm. D-I. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures (viewed from left side), dorsal aspect of penis, ventral aspect of distal penis.

pigment proximally; distal section unpigmented except for central light grey band or uniformly light grey. Snout medium grey to black. Foot light to medium grey or black. Opercular lobe black along inner edge and sides; light to medium grey elsewhere. Neck light to medium grey. Pallial roof, visceral coil uniform black. Ventral penial filament pigmented with scattered black granules.

Ctenidial filaments, 13, weakly pleated, ctenidium

overlapping pericardium posteriorly. Osphradium small, narrow, positioned alongside posterior half of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75-1.0 whorl, filling 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 37A. Albumen gland having short pallial component. Capsule

gland as wide, as long or slightly longer than albumen gland; sub-circular in section; rectal furrow weak. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior oblique loop, often kinked in mid-line, preceded by small posterior twist. Oviduct and bursal duct joining well behind pallial wall; common duct broad. Bursa copulatrix as wide and 67% as long as albumen gland, pyriform, with blunt anterior edge, longitudinal, entire length posterior to gland. Bursal duct originating from anterior edge at mid-line, short, medium width, but broadening distally. Seminal receptacle small, pouchlike, overlapping anterior half of bursa, positioned posterior to albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Prostate gland bean-shaped, pallial portion medium, narrowly ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 37B, C) large; base rectangular, sometimes folded along inner edge; filament slightly shorter than base, medium width, tapering to a pointed tip, longitudinal; lobe medium length, knoblike, longitudinal. Terminal gland large, medium width, curved, transverse, extending onto both dorsal and ventral surfaces. Penial gland usually filling entire length and width of filament, slightly overlapping base. Dg1 small, usually transverse (sometimes circular or oblique), positioned well proximal to penial gland near outer edge. Dg2 small, similar to Dg1 in appearance, sometimes weakly raised, positioned proximally near or along inner edge. Dotlike glands sometimes present near center of lobe (vestige of Dg3?) and just distal to Dg1. Ventral gland large (reduced or absent in some populations), sub-circular, borne on weak swelling, transverse or oblique, positioned near base of filament. Penial duct straight, near outer edge.

**Type locality:** Spring, north-northwest of Holbrook Junction, Antelope Valley, Douglas County, Nevada, T. 10 N, R. 22 E, SW ¼ section 6. Holotype, USNM 873409 (Figure 20M), collected by D. W. Sada, 1 July 1989; paratypes, USNM 860701. The type locality is a small rheocrene impounded several meters below the source.

**Remarks:** A full complement of glands on the penis, including an enlarged penial gland, is found in several other congeners in the region, notably *P. fausta*, but also *P. californiensis* (Gregg & Taylor, 1965) and *P. wongi*. *Pyrgulopsis longiglans* differs from these species in having weakly developed Dg2 and Dg3, and a smaller ventral gland. This species is distributed in the western portion of the Lahontan Basin as well as in adjacent Antelope Valley (Figure 52).

**Material examined:** NEVADA. *Douglas County:* Spring, north-northwest of Holbrook Junction, USNM 873409, USNM 874745.—Spring, 2.4 km south of Dou-

ble Spring, Antelope Valley, T. 11 N, R. 21 E, SW ¼ section 36, USNM 874396, USNM 874753. *Humboldt County:* Spring, 11.3 km west of Double Hot Spring, Black Rock Desert, T. 36 N, R. 25 E, NW ¼ section 5, USNM 874292, USNM 883445.—Spring, 2.3 km west of Wagner Spring, Black Rock Desert, T. 37 N, R. 25 E, NE ¼ section 6, USNM 874295.—Spring, 2.4 km west of Wagner Spring, Black Rock Desert, T. 37 N, R. 25 E, NE ¼ section 6, USNM 874299, USNM 883451.—Spring, 3.2 km west of Bronco Spring, Black Rock Desert, T. 37 N, R. 25 E, NW ¼ section 21, USNM 874297, USNM 883846.—Spring, Jackass Flat, Black Rock Desert, T. 37 N, R. 25 E, NE ¼ section 21, USNM 874288.—Spring, Paiute Creek, Black Rock Desert, T. 40 N, R. 26 E, NW ¼ section 28, USNM 874270.—Spring, Little Smokey Creek, south of road, Black Rock Desert, T. 38 N, R. 23.5 E, NW ¼ section 24, USNM 874223.—Spring, Little Smokey Creek, east of road, Black Rock Desert, T. 38 N, R. 23.5 E, NW ¼ section 24, USNM 874197.—Spring, Little Smokey Creek, north of road, Black Rock Desert, T. 38 N, R. 23.5 E, NW ¼ section 24, USNM 874221.—Spring, Little Smokey Creek, Black Rock Desert, T. 38 N, R. 23.5 E, section 24, USNM 892024.—Spring, Calico Hills, Black Rock Desert, USNM 873223. *Washoe County:* Spring, Hardscrabble Creek, Pyramid Lake Basin, T. 24 N, R. 21 E, SE ¼ section 19, USNM 858276.—Sevenmile Spring, Winnemucca Lake Basin, T. 25 N, R. 23 E, NE ¼ section 9, USNM 874891, USNM 883436.—Spring, southeast of Nugent Springs, Winnemucca Lake Basin, T. 26 N, R. 23 E, SE ¼ section 10, USNM 874904.—Wildcat Spring, North Fork Buffalo Creek, Smoke Creek Desert, T. 34 N, R. 19 E, SW ¼ section 26, USNM 874293.

*Pyrgulopsis militaris*, Hershler, sp. nov.

Northern Soldier Meadow pyrg

(Figures 8G, 15G–I, 21A, B, 37D–F)

**Etymology:** From *militaris* (Latin), of soldiers and war; referring to occurrence of this species in Soldier Meadows, which was named after a U.S. Army camp stationed in the area during the 1860s (Garside & Schilling, 1979: 38).

**Diagnosis:** Small, with sub-globose to ovate-conic shell. Penis large; filament short, lobe medium length. Penial ornament a small terminal gland, small penial gland, large Dg1, small Dg2, small Dg3, 1-2 additional dorsal glands, and medium-sized ventral gland.

**Description:** Shell (Figures 8G, 21A, B) sub-globose to ovate-conic, width/height, 75–92%; height, 1.2–1.9 mm; width, 1.1–1.5 mm; whorls, 3.75–4.25. Protoconch 1.25 whorls, diameter 0.24 mm, surface finely wrinkled (sculpture weakening on later portion, which sometimes has weak spiral elements), sculpture on initial 0.75 whorl

sometimes further developed as pits. Teleoconch whorls medium convexity, shouldered, sometimes having strong sub-sutural angulation on body whorl; body whorl often slightly disjunct behind the aperture in larger specimens. Aperture ovate, angled above; adnate or, more commonly, slightly disjunct. Inner lip sometimes slightly thickened, without columellar shelf. Outer lip thin, orthocline-prosocline, without sinuation. Umbilicus perforate; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface frilled. Attachment scar slightly thickened between nucleus and inner edge and sometimes along portions of outer and/or inner edges.

Radula (Figure 15G-I)  $890 \times 140 \mu\text{m}$ , with 64 rows of teeth. Central tooth  $18 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 5-6; central cusp long and narrow, daggerlike; basal cusps small. Basal tongue broad U-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck weakly flexed; outer wing 190% of cutting edge length. Inner marginal teeth with 23-27 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 25-30 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles unpigmented to medium brown. Snout medium to dark brown or black. Foot, neck light to dark brown. Opercular lobe dark along inner edge, remaining portion medium brown. Pallial roof, visceral coil uniform dark brown or black. Penial filament darkly pigmented internally.

Ctenidial filaments, 15, without pleats, ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5-0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 37D. Albumen gland having very short or no pallial component. Capsule gland longer and slightly narrower or as wide as albumen gland, sub-circular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop preceded by prominent posterior twist. Oviduct and bursal duct joining well behind pallial wall. Bursa copulatrix as long and wide as albumen gland, ovate-pyriform, longitudinal, most of length posterior to gland. Bursal duct originating from anterior edge lateral to mid-line, very short, medium width. Seminal receptacle small, narrow, pouchlike, overlapping middle of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland bean-shaped,

pallial portion short, ovate in section. Proximal pallial vas deferens with well-developed, reflexed loop; duct broad. Penis (Figure 37E, F) large; base rectangular, weakly folded or smooth; filament short, narrow, tapering to point, longitudinal or slightly oblique; lobe a little longer than filament, knoblike, longitudinal. Terminal gland small, narrow, rarely divided into two units, curving, transverse, largely on ventral surface. Penial gland usually filling proximal half of filament (rarely filling entire length), slightly narrower than filament. Dg1 large, borne on prominent swelling, sometimes slightly curved, longitudinal, positioned slightly behind filament. Dg2 small, sub-circular, positioned along inner edge medially. Dg3 small, ovate, positioned along outer edge of lobe. Base rarely bearing small, dotlike gland alongside Dg2 distally. Dorsal surface of lobe also bearing one to two small glands. Ventral gland medium-sized, narrow, borne on prominent pedicel, transverse, positioned near centrally. Penial duct straight, near outer edge.

**Type locality:** Spring, west of Soldier Meadow Ranch, Black Rock Desert drainage, Humboldt County, Nevada, T. 40 N, R. 25 E, SW  $\frac{1}{4}$  section 5. Holotype, USNM 873203 (Figure 21A), collected by J. Jerry Landye, 3 June 1978; paratypes, USNM 860704. The type locality is a small, thermal (30°C.) rheocene that is impounded downstream. This site is Spring Number 2 of Nyquist (1963). Note that the second locality for this species, West Spring in nearby Craine Creek drainage, was only mildly thermal (23°C).

**Remarks:** This snail and the three species locally endemic in Soldier and Mud Meadows drainage compose a well-defined group of *Pyrgulopsis* having a full complement of penial glands, simply coiled oviduct, large bursa copulatrix positioned entirely posterior to the albumen gland, and a small, narrow seminal receptacle. Members of this group also have small, squat shells with weak protoconch sculpture; long, narrow central cusps on the central radular teeth; short penial filament; well-developed, tapered penial lobe; weakly developed terminal gland, and small-medium penial gland. Among the species of this group, *P. militaris* resembles *P. limaria* (described below) in that the penis is endowed with a well-developed penial gland, Dg1, and ventral gland. *Pyrgulopsis militaris* differs from *P. limaria* in that the penis lacks a distal swelling along the inner edge, has a weaker Dg2; and the distal female oviduct is more complexly coiled. The distribution of this species is shown in Figure 52.

**Material examined:** NEVADA. *Humboldt County:* Spring, west of Soldier Meadow Ranch, USNM 860704, USNM 873203, USNM 883991, USNM 892043.—West Spring, Craine Creek drainage, T. 44 N, R. 27 E, NW  $\frac{1}{4}$  section 20, USNM 873156, USNM 883921.



*Pyrgulopsis umbilicata* Hershler, sp. nov.

## Southern Soldier Meadow pyrg

(Figures 8H, 21C, D, 37G–I)

**Etymology:** From *umbilicatus* (Latin), navel; referring to the prominent umbilicus in shells of this species.

**Diagnosis:** Small to medium-sized, with sub-globose to ovate-conic shell. Penis large, filament short, lobe long. Penial ornament a small terminal gland, medium-sized Dg1, large Dg2, small Dg3, and medium-sized ventral gland.

**Description:** Shell (Figures 8H, 21C, D) sub-globose to ovate-conic, width/height, 78–90%; height, 1.7–2.4 mm; width, 1.4–1.9 mm; whorls, 4.0–4.5. Protoconch 1.3 whorls, diameter 0.26 mm, surface usually partly eroded, appearing nearby smooth. Teleoconch whorls highly convex; shoulders weak or absent. Aperture ovate, narrowly adnate. Inner lip thin or slightly thickened, without columellar shelf. Outer lip thin, orthocline, without sinuation. Umbilicus perforate; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface frilled. Attachment scar thick all around.

Radula 1.29 mm × 163 μm, with 72 rows of teeth. Central tooth 18 μm wide, with medium indented dorsal edge; lateral cusps, 4–5; central cusp narrow, daggerlike, basal cusps small, sometimes accompanied by slight thickening to the inside. Basal tongue broad U-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck weakly flexed, outer wing 170% of cutting edge length. Inner marginal teeth with 21–25 cusps; cutting edge occupying 32% of length of tooth. Outer marginal teeth with 26–28 cusps; cutting edge occupying 25% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light to dark grey-brown. Snout medium brown. Foot, neck medium to dark grey-brown. Opercular lobe black along inner edge, otherwise medium brown. Pallial roof, visceral coil uniformly dark brown-black. Ventral surface of penial filament darkly pigmented along proximal half.

Ctenidial filaments, 16, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling 50% of digestive gland behind stomach. Distal female genitalia shown in Figure 37G. Capsule gland slightly shorter to slightly longer, slightly narrower than albumen gland, sub-circular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior ex-

ension. Coiled oviduct a circular to posterior-oblique loop, preceded by weak twist, or weakly kinked at mid-length. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix as long and wide as albumen gland, sub-globose to broadly pyriform, longitudinal, most of length posterior to gland. Bursal duct originating from anterior edge at mid-line, very short, narrow to medium width. Seminal receptacle very small, narrow pouchlike, overlapping anterior or middle portion of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland fat bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop; duct broad. Penis (Figure 37H, I) large; base near square to rectangular, swollen along inner edge distally, weakly folded; filament short, narrow, tapering to point, oblique; lobe often longer than base, tapering, longitudinal. Terminal gland small, narrow-circular, rarely divided into two units, sometimes longitudinal, most of length on ventral surface. Dg1 positioned distally, overlapping as much as proximal half of filament, as wide as filament. Dg2 large, borne on pronounced swelling, sometimes curved (fused?), or accompanied by additional glandular unit (and rarely a second dotlike unit) to outer side, positioned along inner edge distally. Dg3 small, rarely absent, weakly raised, positioned near middle of lobe. Ventral gland medium-sized, narrow, borne on prominent swelling, transverse, positioned on ventral surface of lobe, usually curving onto inner edge of dorsal surface, rarely accompanied by dotlike unit medially. Penial duct straight, near outer edge.

**Type locality:** Spring, near mouth of Warm Springs Canyon, Soldier Meadow, Humboldt County, Nevada, T. 40 N, R. 25 E, NW ¼ section 18. Holotype, USNM 873208 (Figure 21C), collected by J. Jerry Landye, 3 June 1978; paratypes, USNM 860705. The type locality is a small, thermal (36–37°C.) rheocene. This site is Spring Number 6 of Nyquist (1963).

**Remarks:** This snail resembles *P. limaria* (described below) in having a rather long, tapered penial lobe, and highly reduced terminal gland, but differs from this and other species in the Soldier Meadows area in that Dg1 overlaps the penial filament. The distribution of this species is shown in Figure 52.

**Material examined:** NEVADA. *Humboldt County:* Spring, near mouth of Warm Springs Canyon, Soldier Meadow, USNM 860705, USNM 873208, USNM 892044.—Spring, south of above (Spring Number 5 of Nyquist [1963]), Soldier Meadow, T. 40 N, R. 25 E, NW ¼ section 18, USNM 873202, USNM 874922.—Spring, south of Big Hole, Soldier Meadow, T. 40 N, R. 25 E, NW ¼ section 18, USNM 874296, USNM 874896.

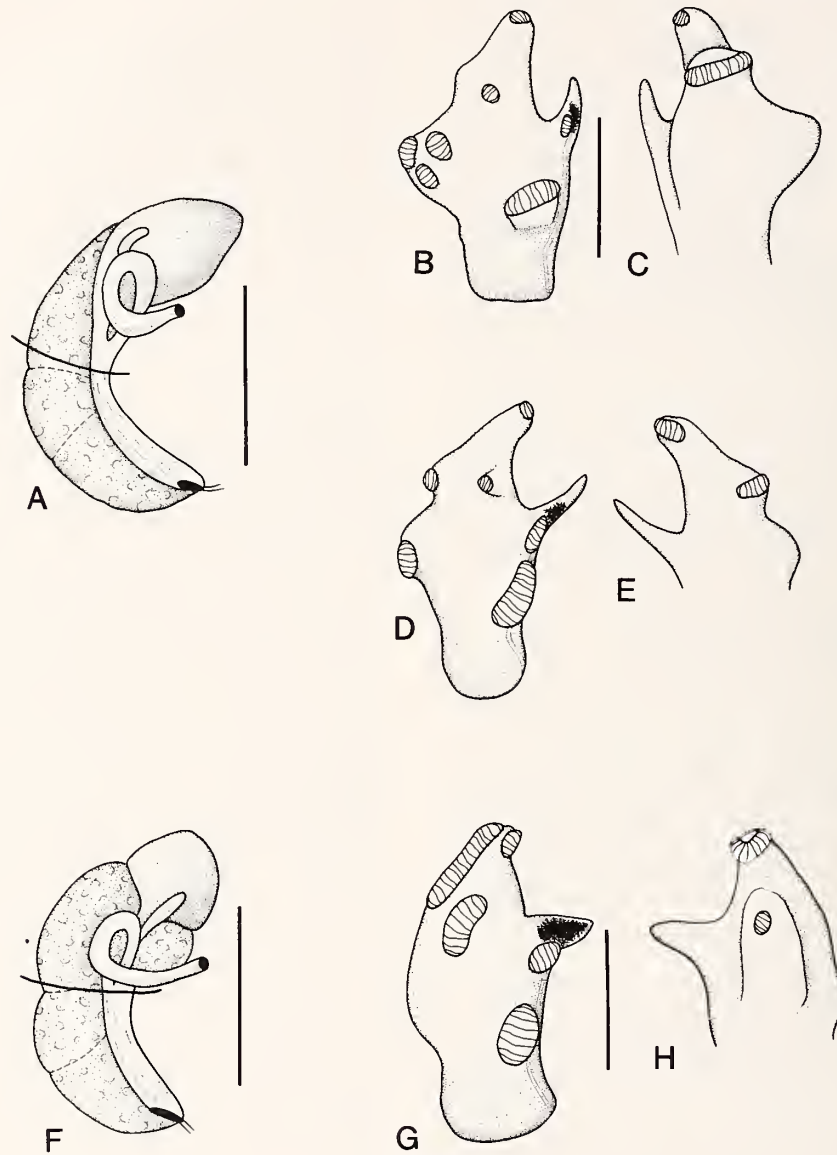


Figure 38

Genitalia of *Pyrgulopsis* species (A–E, *P. limaria*, USNM 860706; F–H, *P. notidicola*, USNM 860707). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two sets of penes (B, C; D, E) are shown for *P. limaria*.

*Pyrgulopsis limaria* Hershler, sp. nov.

Squat Mud Meadows pyrg  
(Figures 8I, 21E–F, 38A–E)

**Etymology:** From *limarius* (Latin), of mud; referring to endemism of this species in Mud Meadows drainage, Nevada.

**Diagnosis:** Small, with low trochoid to ovate-conic shell. Penis large, filament short, lobe medium length. Penial

ornament a small terminal gland, small penial gland, large Dg1; small Dg2, sometimes accompanied by one to two similarly sized glands to outer side; small Dg3, and medium-large ventral gland.

**Description:** Shell (Figures 8I, 21E, F) low trochoid to ovate-conic, width/height, 86–101%; height, 1.3–1.7 mm; width, 1.3–1.6 mm; whorls, 3.75–4.25. Protoconch 1.25 whorls, diameter 0.28 mm, initial 0.75 whorl finely wrinkled (partly eroded), otherwise near smooth. Teleoconch whorls highly convex, strongly shouldered. Aperture

ovate, narrowly adnate or slightly disjunct. Inner lip thin, without columellar shelf. Outer lip thin, orthocone, without situation. Umbilicus deeply perforate. Periostracum tan.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface smooth; outer margin sometimes having very weak rim. Attachment scar slightly thickened between nucleus and inner edge and along inner edge.

Radula 1.15 mm  $\times$  150  $\mu$ m, with 62 rows of teeth. Central tooth 19–24  $\mu$ m wide, with medium indented dorsal edge; lateral cusps, 4–5; central cusp long, narrow, dagger-like; basal cusps small, sometimes accompanied by weak thickenings on inner sides. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck very weakly flexed (nearly straight); outer wing 175% of cutting edge length. Inner marginal teeth with 19–21 cusps; cutting edge occupying 30% of length of tooth, near basal cusp enlarged. Outer marginal teeth with 25–30 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum small.

Cephalic tentacles unpigmented or having light brown patch just proximal to eyes. Snout light to medium brown. Foot unpigmented or very light brown. Opercular lobe dark along inner edge, sometimes along sides. Neck unpigmented except for scattered internal granules. Pallial roof, visceral coil near uniform dark brown. Penial filament darkly pigmented along proximal half.

Ctenidial filaments, 14, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centrally positioned. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 38A. Albumen gland having very short or no pallial component. Capsule gland longer and as wide as albumen gland, sub-circular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a U-shaped or open, posterior-oblique loop. Oviduct and bursal duct joining well behind pallial wall. Bursa copulatrix as long and wide as albumen gland, ovate-pyriform, longitudinal, most of length posterior to gland. Bursal duct originating from anterior edge at or lateral to mid-line, very short, medium width. Seminal receptacle very small, narrow pouchlike, overlapping anterior portion or middle of bursa.

Testis 1.0–1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber anteriorly. Prostate gland ovate, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, often slightly reflexed loop. Penis (Figure 38B–E) large; base rectangular, swollen along inner edge distally; filament

short, narrow, tapering to point, longitudinal or slightly oblique; lobe medium length, clublike, narrowed distally, longitudinal. Terminal gland small, circular or narrow-longitudinal, rarely divided, overlapping ventral slightly more than dorsal surface. Penial gland usually filling less than 50% of filament length, as wide or slightly narrower than filament, sometimes extending slightly onto base, occasionally abutting or fused with Dg1. Dg1 large, borne on pronounced swelling, longitudinal or slightly curving across base, positioned slightly to considerably proximal to filament. Dg2 small, sometimes curved (fused with above?), positioned along inner edge medially, often accompanied by one to two smaller glands on outer side. Dg3 small or dotlike, often borne on raised swelling, positioned near middle of lobe, often accompanied by additional, similarly sized gland. Ventral gland medium-large, rarely divided, borne on prominent swelling, transverse, positioned on basal portion of lobe, sometimes extending onto inner edge of dorsal surface. Penial duct straight, near outer edge.

**Type locality:** Spring brook, Mud Meadow drainage, Humboldt County, Nevada, T. 40 N, R. 24 E, NE  $\frac{1}{4}$  section 26. Holotype, USNM 873232 (Figure 21E), collected by J. Jerry Landye, 30 August 1979; paratypes, USNM 860706. The type locality is a thermal (32°C) spring brook modified to form a drainage ditch. This species also was present at the thermal spring source (ca. 400 m up-flow; 34°C).

**Remarks:** This snail differs from other species in the Soldier Meadows area in having a pronounced swelling along inner edge of penis distally and frequently having small glands adjacent to Dg2.

**Material examined:** NEVADA. *Humboldt County:* Spring brook, Mud Meadow drainage, USNM 860706, USNM 873232, USNM 892045.—Spring brook, 1 km upflow from above, Mud Meadow drainage, T. 40 N, R. 24 E, NE  $\frac{1}{4}$  section 26, USNM 892047.—Spring, Mud Meadow drainage, T. 40 N, R. 24 E, NE  $\frac{1}{4}$  section 23, USNM 874291.

*Pyrgulopsis notidicola* Hershler, sp. nov.

Elongate Mud Meadows pyrg

(Figures 8J, 21G, H, 38F–H)

**Etymology:** From *notis* (Greek), wetness, and *-colus* (Latin), dwelling in; referring to the amphibious habit of this species.

**Diagnosis:** Small to medium-sized, with ovate- to narrow-conic shell. Penis large; filament short, lobe medium length. Penial ornament a large terminal gland, medium-sized penial gland, large Dg1, additional dorsal gland on lobe (not corresponding to either Dg2 or Dg3), and very small ventral gland.

**Description:** Shell (Figures 8J, 21G, H) ovate- to narrow-conic, width/height; 76–96%; height, 1.3–2.4 mm; width, 1.2–1.9 mm; whorls, 3.5–4.25. Protoconch 1.3 whorls, diameter 0.29 mm, initial 0.75 whorl finely wrinkled, otherwise smooth. Teleoconch whorls highly convex, shoulders well developed; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually slightly disjunct. Inner lip slightly thickened, sometimes having narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate, sometimes nearly absent; umbilical region sometimes narrowly excavated. Periostracum tan.

Operculum ovate; nucleus eccentric; dorsal surface very weakly frilled; outer margin sometimes having very weak rim. Attachment scar slightly thickened between nucleus and inner edge and along inner edge.

Radula 1.52 mm × 156 μm, with 75 rows of teeth. Central tooth 25–28 μm wide, with medium indented dorsal edge; lateral cusps, 4–6; central cusp long, narrow, daggerlike; basal cusps medium-sized, sometimes accompanied by weak swelling to inner sides. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 2(3, 4)-1-4(5); neck very weakly flexed or straight; outer wing 160% of cutting edge length. Inner marginal teeth with 23–26 cusps, basal cusps enlarged; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 22–27 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber slightly larger than posterior chamber; stomach caecum very small.

Cephalic tentacles light brown. Snout, foot, light to medium brown. Opercular lobe dark along inner edge, pigment slightly lighter elsewhere. Neck unpigmented or light brown. Pallial roof, visceral coil uniform dark brown-black. Penial filament darkly pigmented internally.

Ctenidial filaments, 17, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland strongly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, abutting posterior edge of stomach. Distal female genitalia shown in Figure 38F. Albumen gland without pallial component. Capsule gland longer and slightly narrower to as wide as albumen gland, sub-circular in section; rectal furrow moderately developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a circular or posterior-oblique loop. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix slightly narrower than albumen gland, medium length, globular, longitudinal, most of length posterior to gland. Bursal duct originating from anterior edge at mid-line,

slightly shorter than bursa, narrow-medium width. Seminal receptacle small, narrow, digitate, overlapping anterior or middle of bursa.

Testis 0.75–1.0 whorl, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland ovate, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 38G, H) large; base rectangular, slightly swollen along inner edge distally, smooth or weakly folded; filament short, broadly triangular, tapering to point, oblique; lobe slightly shorter than base, knoblike, distally narrowed, longitudinal. Terminal gland large, narrow, transverse, extending along much of outer edge of lobe, curving onto both surfaces. Penial gland filling proximal portion of filament and extending onto base, as wide as filament. Dg1 large, fairly broad, weakly raised, longitudinal, positioned near middle of base. Dorsal lobe bearing narrow gland basally. Ventral gland very small, circular-ovate, borne on raised swelling, sometimes longitudinal, positioned at base of lobe. Penial duct straight, near outer edge.

**Type locality:** Spring, Mud Meadow drainage, Humboldt County, Nevada, T. 40 N, R. 24 E, NW ¼ section 23. Holotype, USNM 873215 (Figure 21G), collected by J. Jerry Landye, 30 August 1979; paratypes, USNM 860707. The type locality area is the northernmost of a large series of thermal springs having broad outflows (e.g., Figure 3B). Water temperature at the sources of these springs was about 50°C. *Pyrgulopsis notidicola* was collected from moistened zones on emergent rocks (snails were much less abundant in the water). Downflow from source springs, where the water cooled to about 40°C, snails were still predominantly found out of the water. The madicolous habit of snails at the type locality was paralleled at the other two sites.

**Remarks:** This snail is distinguished from other species in the Soldier Meadows area by its more elongate shell with short spire, larger and more disjunct aperture, well-developed columellar shelf; smaller, globose bursa copulatrix; and penis with larger terminal gland, and very weak ventral gland.

**Material examined:** NEVADA. *Humboldt County:* Spring, Mud Meadow drainage, USNM 860707, USNM 873215, USNM 892048.—Spring (tub area), Mud Meadow drainage, T. 40 N, R. 24 E, NW ¼ section 23, USNM 874294.—Old gauge box, 0.8 km southwest of above, Mud Meadow drainage (Figure 3B), T. 40 N, R. 24 E, NW ¼ section 23, USNM 874286.

*Pyrgulopsis vinyardi* Hershler, sp. nov.

Vinyards pyrg

(Figures 8K, 21I, 39A–C)

**Etymology:** Named after Gary Vinyard (University of Nevada, Reno), in recognition of his assistance with field surveys in northwest Nevada.

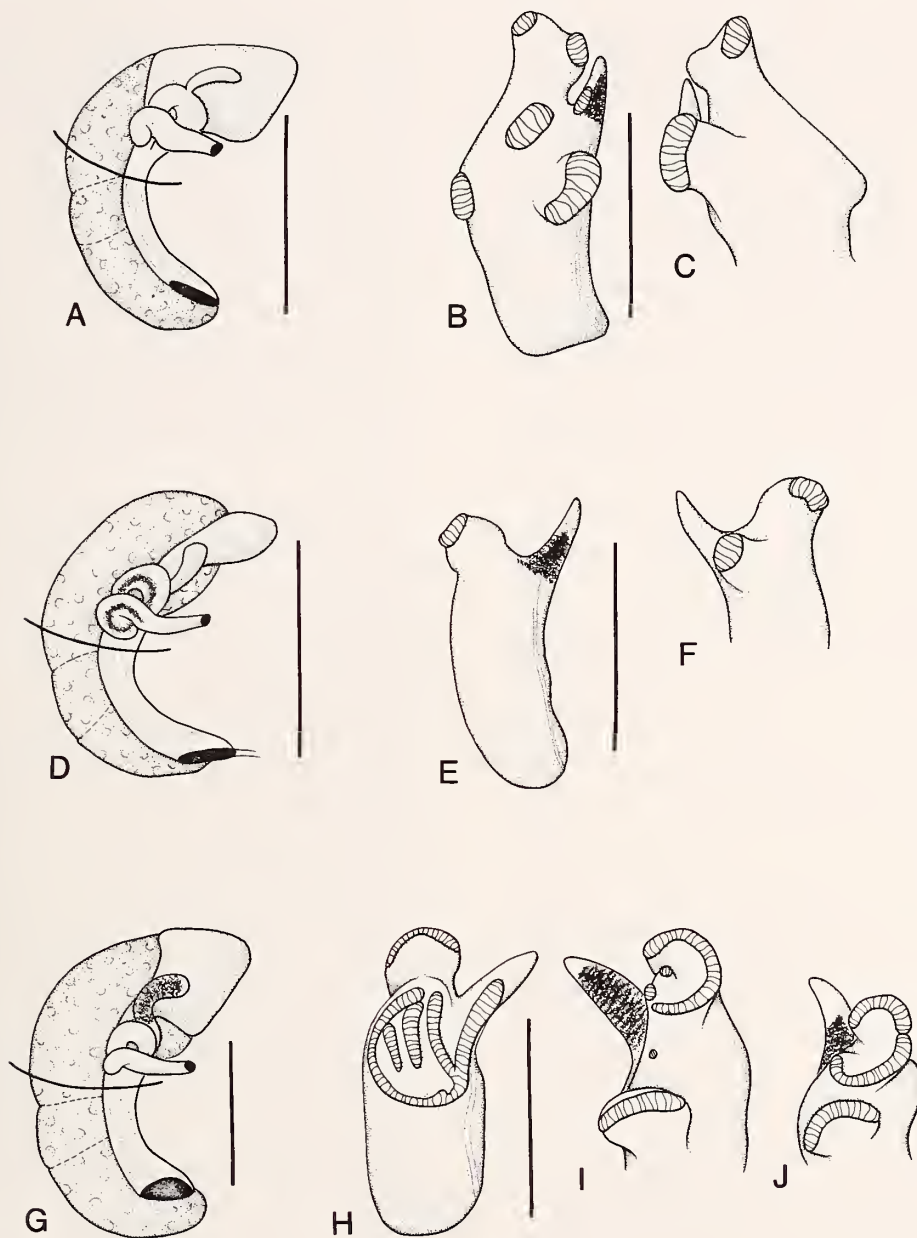


Figure 39

Genitalia of *Pyrgulopsis* species (A–C, *P. vinyardi*, USNM 874739; D–F, *P. imperialis*, USNM 874744; G–I, *P. sadai*, USNM 883857; J, *P. sadai*, USNM 883851). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two examples of the ventral penis (I, J) are shown for *P. sadai*.

**Diagnosis:** Small, with sub-globose to ovate-conic shell. Penis large, filament short, lobe medium length. Penial ornament a small terminal gland, small penial gland, large Dg1, small Dg2, small Dg3, additional dorsal gland on lobe, and large ventral gland.

**Description:** Shell (Figures 8K, 21I) sub-globose to

ovate-conic, width/height, 75–92%; height, 1.6–2.0 mm; width, 1.3–1.6 mm; whorls, 3.5–4.0. Protoconch 1.2 whorls, diameter 0.21 mm, surface eroded. Teleoconch whorls medium to highly convex, shoulders well developed; body whorl often slightly disjunct behind the aperture. Aperture ovate, often expanded; broadly adnate or

slightly disjunct. Inner lip slightly thickened, sometimes having narrow columellar shelf. Outer lip thin, prosocline, weakly sinuate. Umbilicus narrowly rimate; umbilical region sometimes narrowly excavated. Periostracum yellow-tan.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar slightly thickened between nucleus and inner edge.

Radula  $790 \times 120 \mu\text{m}$ , with 63 rows of teeth. Central tooth  $14 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 6–7; central cusp long, narrow, daggerlike; basal cusps medium-sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck weakly flexed or absent; outer wing 210% of cutting edge length. Inner marginal teeth with 21–25 cusps (basal cusp enlarged); cutting edge occupying 35% of length of tooth. Outer marginal teeth with 25–30 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout, foot, neck light to medium grey-brown. Opercular lobe unpigmented or sometimes black along inner edge or all around. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented along most of length.

Ctenidial filaments, 14, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered slightly posterior to middle of ctenidium. Kidney opening white, thick. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, abutting or overlapping posterior stomach chamber. Distal female genitalia shown in Figure 39A. Albumen gland having short pallial component. Capsule gland longer than and as wide as albumen gland, ovate in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold weak. Genital aperture an elongate, terminal slit without anterior extension. Coiled oviduct a small posterior-oblique loop preceded by well-developed posterior twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix longer than and as wide as albumen gland, broadly ovate to pyriform, longitudinal, with almost entire length posterior to gland. Bursal duct originating from anterior edge at mid-line or slightly dorsal to mid-line, very short, medium width. Seminal receptacle small, narrow, overlapping middle of bursa copulatrix, entering dorsal portion of oviduct coil.

Testis 1.0–1.25 whorls, filling 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland elongate bean-shaped, pallial portion medium, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 39B, C) large; base rectangular, distally expanded along inner edge, smooth; filament short, narrow, tapering to point, slightly oblique; lobe as long or slightly longer than fil-

ament, knoblike, often distally bifurcate, longitudinal. Terminal gland small, sub-circular, transverse, curving, positioned along inner edge of distal lobe with most of length on ventral surface. Penial gland filling inner portion of proximal half of filament, 50% as wide as filament. Dg1 large, broad, rarely divided into two units, crescent-shaped, borne on prominent swelling, usually longitudinal, positioned a little behind base of filament. Dg2 dotlike or small (rarely absent), narrow, positioned medially along expanded inner edge. Dg3 small (rarely dotlike), circular, positioned along outer edge of lobe distally. Dorsal surface of lobe also bearing narrow, oblique-longitudinal gland medially. Ventral gland large, borne on very prominent swelling, longitudinal, positioned along-side base of filament. Penial duct straight, near outer edge.

**Type locality:** Spring, Willow Creek, 1.6 km southwest of Willow Creek Reservoir, Squaw Valley drainage, Elko County, Nevada, T. 39 N, R. 48 E, NE  $\frac{1}{4}$  section 33. Holotype, USNM 874740 (Figure 211), collected by G. Vinyard, 5 June 1992; paratypes, USNM 860708. The type locality is a shallow, but broad rheocrene flowing out of a steep hillside.

**Remarks:** This snail closely resembles the group of locally endemic species in Soldier Meadows, especially *P. militaris*, which has a similar pattern of penial ornament and shape of oviduct coil. *Pyrgulopsis vinyardi* differs from this species in its larger shell aperture, frequent presence of a columellar shelf, and penis with smaller penial gland and prominent pedicel of the ventral gland. Animal from the type locality were highly parasitized, hence specimens from the second locality were used for anatomical study. The distribution of this species is shown in Figure 52.

**Material examined:** NEVADA. *Elko County:* Spring, source of Hot Creek, Squaw Valley drainage, T. 38 N, R. 48 E, SE  $\frac{1}{4}$  section 11, USNM 874739.—Spring, Willow Creek, 1.6 km southwest of Willow Creek Reservoir, T. 39 N, R. 48 E, NE  $\frac{1}{4}$  section 33, USNM 860708, USNM 874740.

*Pyrgulopsis imperialis* Hershler, sp. nov.

Kings River pyrg

(Figures 8L, 21J, K, 39D–F)

**Etymology:** From *imperialis* (Latin), of the empire or emperor; referring to the endemism of this species in Kings River Valley, Nevada.

**Diagnosis:** Small, with ovate- to narrow-conic shell. Penis large, filament and lobe medium length. Penial ornament a small length terminal gland and small ventral gland.

**Description:** Shell (Figures 8L, 21J, K) ovate- to narrow-

conic, near pupiform, width/height, 63–82%; height, 1.4–1.8 mm; width, 1.0–1.4 mm; whorls, 3.75–4.25. Protoconch 1.25 whorls, diameter 0.29 mm, initial 0.5–0.75 whorl finely wrinkled (mostly along inner edge), otherwise smooth. Teleoconch whorls slightly-moderately convex; body whorl often slightly disjunct behind the aperture. Aperture ovate, strongly angled above, disjunct. Inner lip thick, without columellar shelf. Outer lip slightly thickened, orthocone or weakly prosocline, slightly sinuate. Umbilicus narrowly rimate to perforate. Periostracum tan.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface smooth; outer margin having weak to well-developed rim. Attachment scar thick along inner edge, sometimes similarly so along a portion or remainder of perimeter.

Radula  $760 \times 125 \mu\text{m}$ , with 57 rows of teeth. Central tooth  $14 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 5–7 (sometimes fused dorsally); central cusp narrow, daggerlike; basal cusps small. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3(4, 5)-1-5; neck weakly flexed; outer wing 275% of cutting edge length. Inner marginal teeth with 21–26 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 28–31 cusps; cutting edge occupying 26% of length of tooth. Stomach longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles, snout, foot, neck light to medium grey. Opercular lobe medium to dark grey-black all around, central area lighter. Pallial roof, visceral coil uniform black. Proximal half of penial filament darkly pigmented internally.

Ctenidial filaments, 12, without pleats; ctenidium overlapping pericardium posteriorly, osphradium small, narrow, centered slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 39D. Albumen gland having short pallial component. Capsule gland as long and wide as albumen gland, ovate in section; rectal furrow moderately developed. Ventral channel moderately overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two overlapping, posterior-oblique or circular coils (anterior portion sometimes only twisted); oviduct walls invested with dark pigment. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, narrow, ovate or subglobular, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at midline, almost as long as bursa, medium width. Seminal receptacle small to medium-sized, narrow, overlapping anterior half of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and most of anterior stomach chambers. Prostate gland small, bean-shaped, pallial portion very short, narrowly ovate in section. Proximal pallial vas deferens straight or having weak bend. Penis (Figure 39E, F) large; base elongate-rectangular, smooth or weakly folded along inner edge; filament medium length and width, tapering to point, longitudinal or slightly oblique; lobe as long as filament, knoblike, longitudinal or slightly oblique. Terminal gland small, rectangular, sometimes divided into two units, sometimes weakly curved, transverse, overlapping dorsal and ventral surfaces. Dotlike distal Dg3 seen in one specimen. Ventral gland small, sub-circular, borne on swelling alongside base of filament. Penial duct straight, near outer edge.

**Type locality:** Spring, south side of road, Thacker Pass, Kings River Valley, Humboldt County, Nevada, T. 44 N, R. 34 E, NE  $\frac{1}{4}$  section 14 (Figure 53). Holotype, USNM 874207 (Figure 21J), collected by G. Vinyard, 24 June 1991; paratypes, USNM 860716. The type locality is a small, highly vegetated rheocene arising from the side of a steep hill.

**Remarks:** This snail differs from other species in the genus in which the penis is solely ornamented with terminal and ventral glands by the combination of small size, fairly narrow shell, moderately elongate lateral wing on the lateral radular teeth, and pigmented coiled oviduct.

**Material examined:** NEVADA. *Humboldt County:* Spring, south side of road, Thacker Pass, USNM 860716, USNM 874207, USNM 874744.—Spring, north side of road, Thacker Pass, Kings River Valley, T. 44 N, R. 34 E, SE  $\frac{1}{4}$  section 11, USNM 874211.

*Pyrgulopsis sadai* Hershler, sp. nov.

Sada's pyrg

(Figures 9A, 21L–N, 39G–J)

**Etymology:** Named after Don Sada, in recognition of his assistance with field surveys throughout the western portion of the Great Basin.

**Diagnosis:** Medium-sized, with sub-globose to ovate-conic shell. Penis large; filament and lobe medium length. Penial ornament a large terminal gland, large penial gland; large, fused Dg1–2, additional two to five dorsal glands, and two large ventral glands.

**Description:** Shell (Figures 9A, 21L–N) sub-globose to ovate-conic, width/height, 68–88%; height, 2.0–3.3 mm; width, 1.6–2.3 mm; whorls, 3.75–4.75. Protoconch 1.3 whorls, diameter 0.33 mm, surface near smooth. Teleoconch whorls medium convexity, shoulders well developed. Aperture ovate, usually broadly adnate. Inner lip thick in largest specimens, without columellar shelf. Out-

er lip thin, slightly prosocline, weakly sinuate. Umbilicus rimate to narrowly perforate. Periostracum tan-brown.

Operculum ovate, amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar broadly thickened along all or most of margin.

Radula  $590 \times 100 \mu\text{m}$ , with 60 rows of teeth. Central tooth  $26 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 5–7; central cusp medium width, daggerlike; basal cusps small, sometimes accompanied by minute cusps to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 25–29 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 32–34 cusps; cutting edge occupying 25% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light to medium grey-brown, sometimes almost black. Snout medium to dark grey-brown. Foot, neck light to medium grey-brown. Opercular lobe medium grey-black all around, central region lighter. Pallial roof, visceral coil medium grey to uniform black. Penial filament darkly pigmented.

Ctenidial filaments, 20, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered posterior to middle of ctenidial axis. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 39G. Albumen gland having short or no pallial component. Capsule gland slightly shorter to as long, as wide as albumen gland, sub-ovate in section; rectal furrow well developed. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a sub-terminal pore without anterior extension. Coiled oviduct a posterior-oblique loop usually preceded by posterior-oblique twist or small loop. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length, slightly narrower than albumen gland, elongate-pyriform, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, short, medium width to broad. Seminal receptacle small, narrow pouch, darkly pigmented internally, often folded, overlapping anterior half of bursa.

Testis 1.0–1.25 whorls, filling 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 39H–J) large; base rectangular, smooth; filament slightly shorter than base, medium width, tapering to point, longitudinal or slightly oblique; lobe shorter than filament, knoblike, longitudinal. Terminal gland large, narrow, crescentlike, sometimes comprising three abutting or closely adjacent

units, transverse, curving onto ventral surface, abutting or fused with distal ventral gland. Penial gland filling most of length of filament, as wide as filament, extending onto base. Dg1 and Dg2 fused into large crescentlike unit crossing penis (proximal to filament) and extending distally where it may again cross the penis toward the filament (where it is borne on an obvious swelling); sometimes forming a completely closed circle, often also fused with penial gland. Dorsal penis having two to five additional elongate, longitudinal glands (sometimes fragmented and/or accompanied by one to two small, dotlike units) lying within circle formed by gland described above; glands may be variously fused with each other as well as with main crescentlike gland. (Dg3 was never seen as separate unit, but may be fused with Dg1–2, or possibly be represented by one of the longitudinal units enclosed by the above.) Proximal ventral gland large, narrow, borne on large swelling, transverse, positioned proximal to filament; distal gland slightly smaller, narrow, similarly borne on swelling, transverse. Space between ventral glands sometimes having dotlike gland. Penial duct straight, near outer edge.

**Type locality:** Spring, Moss Creek, Reese River Valley, Lander County, Nevada, T. 27 N, R. 44 E, SE  $\frac{1}{4}$  section 16. Holotype, USNM 874397 (Figure 21L), collected by D. W. Sada, 10 September 1991; paratypes, USNM 860702. The type locality area is a complex of small, shallow (but having broad expanse) rheocrenes, all of which were seriously degraded by livestock (Figure 5A). Only a single spring in the complex contained this species, which was found in an area of less than  $1 \text{ m}^2$ .

**Remarks:** This snail resembles several other Great Basin species (*P. californiensis*, *P. longinqua*, *P. wongi*) in that the penis has a full complement of penial glands, with the main dorsal glands fused to form a U-shaped unit, within which are a series of additional longitudinal glands. *Pyrgulopsis sadai* further resembles *P. wongi* in having a distal, curved ventral gland which often is fused or abutting the terminal gland. *Pyrgulopsis sadai* differs from these species in having a moderately broad shell (that of *P. wongi* is broader while that of *P. californiensis* and *P. longinqua* is more attenuate) and strongly pigmented seminal receptacle. This species is found in the central part of the Lahontan Basin as well as in drainage of the Owyhee River (Figure 53).

**Material examined:** NEVADA. *Humboldt County:* Spring, Tony Creek, Silver State–Quinn River Valley, T. 40 N, R. 38 E, SW  $\frac{1}{4}$  section 4, USNM 874754, USNM 874208, USNM 883995.—Maiden Springs, Little Owyhee River drainage, T. 45 N, R. 42 E, SE  $\frac{1}{4}$  section 3, USNM 883900, USNM 883999. *Lander County:* Spring, Moss Creek (Figure 5A), USNM 860702, USNM 874397, USNM 883857.—Spring, Moss Creek, Reese River Valley, T. 27 N, R. 44 E, center section 13, USNM 883851.—Spring,



Willow Creek, Buffalo Valley, T. 32 N, R. 43 E, SE ¼ section 32, USNM 874408.—Spring, Daisy Creek, Buffalo Valley, T. 27 N, R. 41 E, SE ¼ section 9, USNM 874392. *Pershing County*: Buffalo Springs, Buffalo Valley, T. 30 N, R. 41 E, SW ¼ section 31, USNM 874388.

*Pyrgulopsis augustae* Hershler, sp. nov.

Elongate Cain Spring pyrg

(Figures 9B, 22A, 40A, B)

**Etymology:** Referring to local endemism of this snail in the foothills of the Augusta Mountains, Nevada.

**Diagnosis:** Medium-sized, with narrow-conic shell. Penis medium-sized, bladelike; filament short, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 9B, 22A) narrow-conic, width/height, 60–66%; height, 2.1–2.6 mm; width, 1.3–1.6 mm; whorls, 4.25–5.25. Protoconch 1.25 whorls, diameter 0.29 mm, early portion finely wrinkled, later surface near smooth, entire surface often eroded. Teleoconch whorls slightly convex, sometimes almost flat, narrowly shouldered; body whorl often slightly disjunct behind the aperture. Aperture ovate, strongly angled above; broadly adnate or slightly disjunct. Inner lip slightly thickened in largest specimens, without columellar shelf. Outer lip thin, orthocone or slightly prosocline, without sinuation. Umbilicus rimate, shell rarely anomphalous. Periostracum light tan.

Operculum ovate, light amber; nucleus eccentric; dorsal surface frilled; outer margin sometimes having weak rim. Attachment scar thickened between nucleus and inner edge.

Radula 840 × 135 μm, with 53 rows of teeth. Central tooth 21 μm wide, with medium indented dorsal edge; lateral cusps, 4–5; central cusp medium width, dagger-like; basal cusps medium-sized. Basal tongue broad V-shaped, sometimes terminating with distinct, small, U-shaped component; basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck weakly flexed; outer wing 160% of cutting edge length. Inner marginal teeth with 19–22 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 22–28 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented, but usually having light to medium grey-brown stripe proximally. Snout nearly unpigmented to medium brown. Foot unpigmented or very light brown. Opercular lobe usually having medium grey streak along inner edge, sometimes similarly pigmented along sides. Neck unpigmented except for scattered grey-brown granules to medium grey. Pallial roof, visceral coil medium to dark grey-brown, pigment lighter on ventral surface. Distal base of penis and proximal filament having medium (internal) brown pigment.

Ctenidial filaments, 17, weakly pleated; ctenidium connected to pericardium by short efferent vessel. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 40A. Albumen gland having short pallial component. Capsule gland shorter and narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two small, overlapping posterior-oblique loops. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix short, medium width, ovate-pyriform, longitudinal or oblique, 50% of length posterior to gland; dorsal edge sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at or lateral to mid-line, as long as bursa, medium width. Seminal receptacle small, narrow, sometimes folded, overlapping anterior bursa or proximal portion of bursal duct.

Testis 1.5 whorls, filling 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland very small, bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens straight or having small, weak bend. Penis (Figure 40B) medium-sized; base elongate-rectangular, smooth; filament short, tapering to point, medium width, longitudinal, weakly distinguished from base by slight constriction; lobe absent, distal edge of penis gently tapering; glands absent. Penial duct straight, near outer edge.

**Type locality:** Cain Spring, Antelope Valley, Lander County, Nevada, T. 25 N, R. 40 E, SW ¼ section 5 (Figure 53). Holotype, USNM 874402 (Figure 22A), collected by D. W. Sada, 10 September 1991; paratypes, USNM 860687. The type locality is a small rheocene in which *Pyrgulopsis augustae* co-occurs with *P. pictilis* (described below).

**Remarks:** This species is contrasted with *P. dixensis* above.

**Material examined:** NEVADA. *Lander County*: Cain Spring, USNM 860687, USNM 874402.

*Pyrgulopsis pictilis* Hershler, sp. nov.

Ovate Cain Spring pyrg

(Figures 9C, 22B, C, 40C–E)

**Etymology:** From *pictilis* (Latin), colored; referred to the strong pigmentation of the female seminal receptacle in this species.

**Diagnosis:** Medium-sized, with broadly to ovate-conic

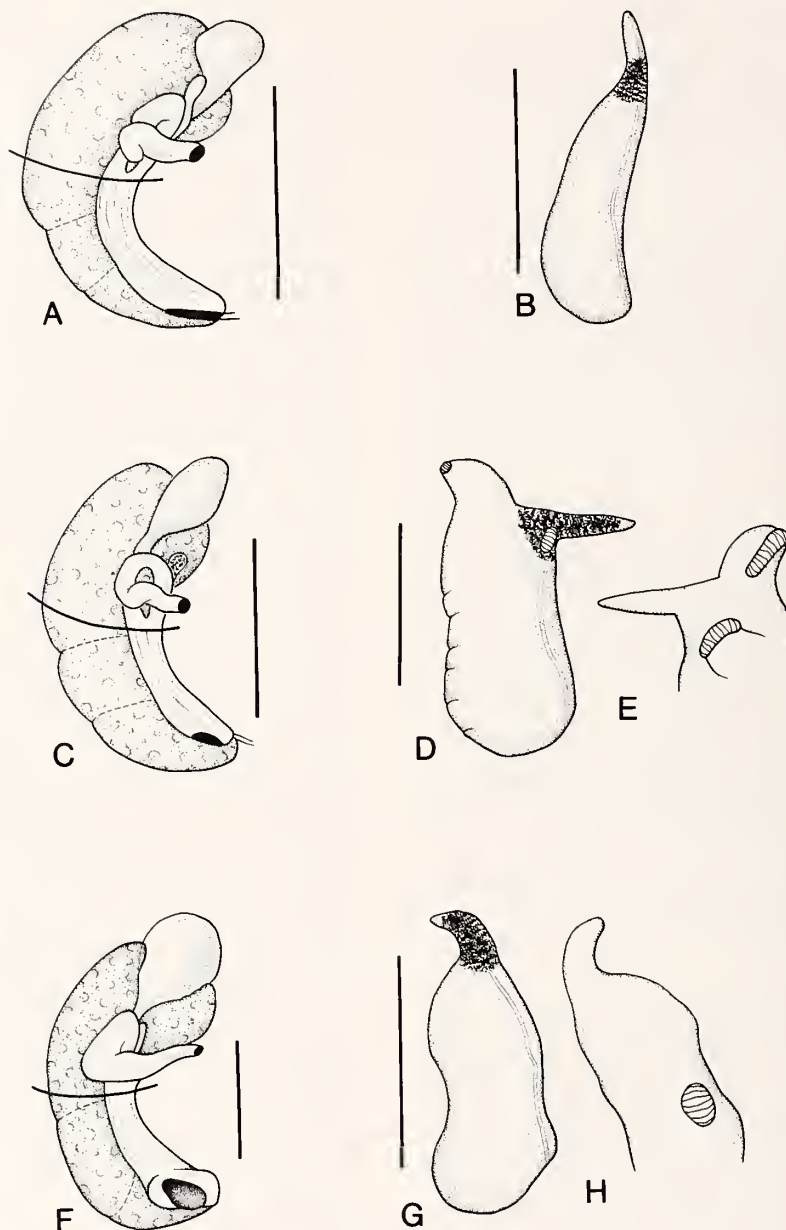


Figure 40

Genitalia of *Pyrgulopsis* species (A, B, *P. augustae*, USNM 860687; C-E, *P. pictilis*, USNM 860713; F-H, *P. basiglans*, USNM 860692). A-E. Bars = 0.5 mm. F. Bar = 0.25 mm. G, H. Bar = 0.25 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. augustae* as this species lacks ornament).

shell. Penis large; filament and lobe medium length. Penial ornament a medium-sized terminal gland, very small penial gland, and small ventral gland.

**Description:** Shell (Figures 9C, 22B, C) broadly to ovate-conic, width/height, 77–86%; height, 2.0–2.7 mm; width, 1.7–2.2 mm; whorls, 4.0–4.75. Protoconch 1.25 whorls, diameter 0.33 mm; surface smooth except for occasional

very weak wrinkling at apex. Teleoconch whorls highly convex, often broadly shouldered. Aperture ovate, broadly adnate or narrowly disjunct. Inner lip slightly thick, sometimes having narrow columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate or narrowly perforate. Periostracum tan.

Operculum ovate, amber, nuclear region darker; nucle-

us eccentric; dorsal surface smooth; outer margin having weak rim. Attachment scar slightly thickened between nucleus and inner edge.

Radula  $640 \times 110 \mu\text{m}$ , with 54 rows of teeth. Central tooth  $28 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 6–7; central cusp medium width, daggerlike, basal cusps medium-sized. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed, outer wing 167% of cutting edge length. Inner marginal teeth with 26–29 cusps; cutting edge occupying 35% of length of tooth. Outer marginal teeth with 33–39 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles nearly unpigmented to light brown. Snout light grey-brown. Foot light to medium grey-brown. Opercular lobe dark along inner edge, sometimes all around. Neck light to medium grey. Pallial roof, visceral coil dark brown-black, pigment lighter on genital ducts. Penial filament darkly pigmented along most of length; distal penis adjacent to filament similarly pigmented. Penial lobe sometimes having scattered black granules.

Ctenidial filaments, 17, pleated, ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered posterior to middle of ctenidium. Renal gland oblique; kidney opening slightly thickened. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.75–1.25 whorl, filling 50% or slightly less of digestive gland behind stomach, abutting posterior edge of stomach anteriorly. Distal female genitalia shown in Figure 40C. Albumen gland having very short pallial component. Capsule gland slightly shorter, narrower than albumen gland, ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop preceded by weak twist or small posterior-oblique coil. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix short, medium width, narrowly ovate, longitudinal, 33–50% of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line, 50–67% length of bursa, medium width. Seminal receptacle small, pouchlike, darkly pigmented, overlapping or ventral to proximal bursal duct and (sometimes) anteriormost bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland very small, ovate or weakly bean-shaped, entirely visceral or with very short pallial portion, narrowly ovate in section. Proximal pallial vas deferens having well-developed loop. Penis (Figure 40D, E) large; base elongate-rectangular, weakly folded; filament medium length, narrow, tapering to point, slightly

oblique; lobe medium length, clublike, longitudinal. Terminal gland medium-sized, narrow, slightly curved, transverse, largely on ventral surface. Penial gland small, 50% as wide as filament, positioned along outer edge of proximal filament, sometimes slightly overlapping base distally. Single specimen having dotlike gland along outer edge of penis distally (corresponding to Dg2). Ventral gland small (absent in one specimen), transverse or oblique, borne on swelling, positioned alongside base of filament. Penial duct straight, near outer edge.

**Type locality:** Cain Spring, Antelope Valley, Lander County, Nevada, T. 25 N, R. 40 E, SW  $\frac{1}{4}$  section 5 (Figure 53). Holotype, USNM 874401 (Figure 22B), collected by D. Sada, 10 September 1991; paratypes, USNM 860713.

**Remarks:** This species closely resembles *P. humboldtensis* (described below) in penial form and pattern of ornament, but is distinguished by its weaker operculum attachment scar, more numerous cusps on the marginal radular teeth, broader penial filament, longer bursal duct, and pigmented seminal receptacle. The single sample of this species contained only three males.

**Material examined:** NEVADA. *Lander County:* Cain Spring, USNM 860713, USNM 874401.

*Pyrgulopsis basiglans* Hershler sp. nov.

Large gland Carico pyrg

(Figures 9D, 13D, 22D, 40F–H)

**Etymology:** From *basis* (Latin), bottom; *glans*, gland; referring to the unusual basal position of the ventral gland of the penis of this species.

**Diagnosis:** Small, with sub-globose to ovate-conic shell. Penis large, filament short, lobe absent. Penial ornament a medium-sized ventral gland.

**Description:** Shell (Figures 9D, 22D) sub-globose to ovate-conic, width/height, 73–87%; height, 1.3–1.8 mm; width, 1.1–1.3 mm; whorls, 3.5–4.5. Protoconch 1.2–1.25 whorls, diameter 0.28 mm, surface smooth except for fine wrinkling near apex and widely spaced, weak spiral striae on final 0.5 whorl. Teleoconch whorls highly convex, shoulders well developed, often broad; body whorl often slightly disjunct behind the aperture. Aperture ovate; narrowly adnate or disjunct. Inner lip thin, without columellar shelf. Outer lip thin, prosocline, without situation. Umbilicus perforate. Periostracum tan.

Operculum (Figure 13D) ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface frilled; outer margin having weak rim. Attachment scar broadly thickened all around.

Radula  $760 \times 120 \mu\text{m}$ , with 67 rows of teeth. Central tooth  $17 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 5–7; central cusp narrow, daggerlike; basal

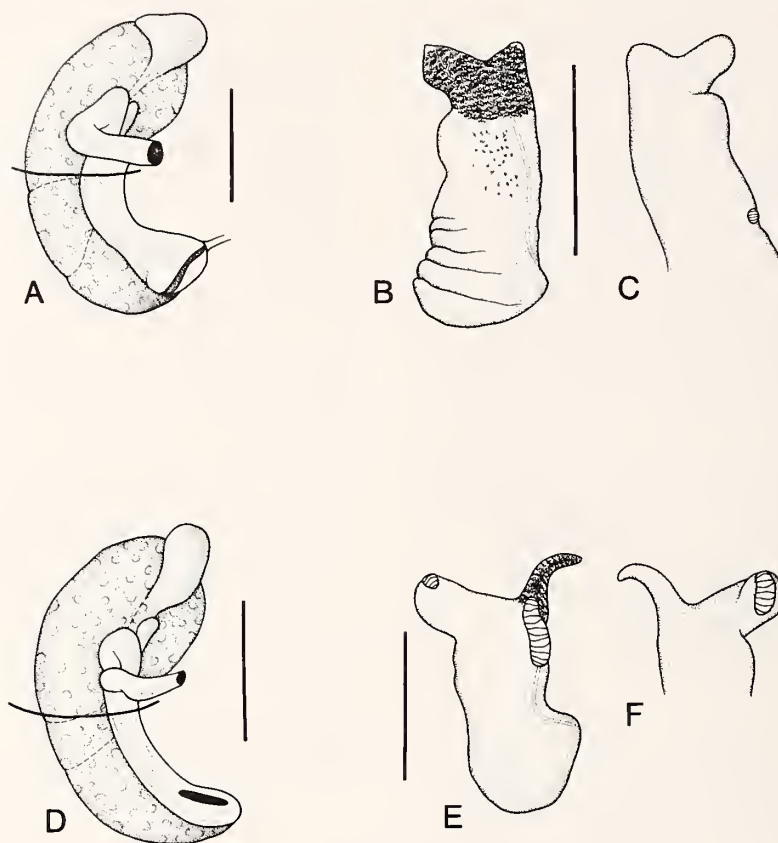


Figure 41

Genitalia of *Pyrgulopsis* species (A–C, *P. bifurcata*, USNM 860693; D–F, *P. pellita*, USNM 860715). A. Bar = 0.25 mm. B–F. Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Note the bifurcate penial filament of *P. bifurcata*.

cusps medium-sized. Basal tongue broad V-shaped, basal sockets deep. Lateral tooth formula 4(5)-1-4(5); neck weakly flexed or absent; outer wing 230% of cutting edge length. Inner marginal teeth with 24–30 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 29–34 cusps; cutting edge occupying 25% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach chamber very small.

Cephalic tentacles, snout light to medium grey-brown. Foot, neck light grey. Opercular lobe light to medium grey-brown, pigment diffuse. Pallial roof, visceral coil uniform black. Penial filament darkly pigmented internally.

Ctenidial filaments, 12, weakly pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 40F. Al-

bumen gland having short or no pallial component. Capsule gland as long, but narrower than albumen gland, sub-circular in section, rectal furrow absent. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a large terminal pore mounted on a swollen and slightly raised papilla; anterior extension absent. Coiled oviduct a posterior-oblique loop sometimes kinked at mid-length. Oviduct and bursal duct joining just behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, sometimes overlapped by gland anteriorly, 50% of length posterior to gland. Bursal duct originating from anterior edge at midline, 50–75% length of bursa, medium width (often expanded distally), sometimes overlapped by albumen gland proximally. Seminal receptacle minute, narrow, overlapping proximal bursal duct.

Testis 1.0 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, weakly reflexed loop. Pe-

nis (Figure 40G, H) large; base rectangular, inner edge usually expanded distally, smooth; filament short, curved, medium width, tapering to point, longitudinal; lobe absent. Distal edge of penis tapering toward base of filament. Ventral gland medium-sized, ovate, longitudinal, positioned near inner edge proximally. Penial duct straight, near outer edge.

**Type locality:** Spring, Cooks Creek, Carico Lake Basin, Lander County, Nevada, T. 27 N, R. 45 E, NE¼ section 27. Holotype, USNM 874280 (Figure 22D), collected by R. Hershler, 26 July 1991; paratypes, USNM 860692. The type locality is a broad rheocene heavily impacted by livestock grazing.

**Remarks:** Among species having penial ornament solely consisting of a superficial ventral gland, this species and *Pyrgulopsis bifurcata* (described next), also locally endemic in Carico Lake Basin, compose a distinct group in which the ventral gland is small and positioned near the inner edge proximally. These species are further united by small, broad to ovate-conic shell, moderately sculptured protoconch having spiral striae on later portion, thick operculum attachment scar; deeply indented central radular teeth with slender, elongate central cusps and deep basal sockets; and distal female genitalia having a simple oviduct coil; very small, narrow, seminal receptacle; and raised and expanded distal end of ventral channel. *Pyrgulopsis basiglans* differs from *P. bifurcata* in the larger ventral gland on the penis, absence of a penial lobe, and ovate (not pyriform) bursa copulatrix. The distribution of this species is shown in Figure 53.

**Material examined:** NEVADA. *Lander County:* Spring, Cooks Creek, USNM 860692, USNM 874280.—Springs, southeast side of Carico Lake, Carico Lake Basin, T. 26 N, R. 45 E, NE¼ section 15, USNM 874304.

*Pyrgulopsis bifurcata* Hershler, sp. nov.

Small gland Carico pyrg

(Figures 9E, 22E, 41A–C)

**Etymology:** From *furcatus* (Latin), forked; referring to the unusual, bifurcate aspect of the distal end of the penis in this species.

**Diagnosis:** Small, with broadly- to ovate-conic shell. Penis large, filament and lobe short. Penial ornament a very small ventral gland.

**Description:** Shell (Figures 9E, 22E) broadly to ovate-conic, width/height, 70–83%; height, 1.3–1.8 mm; width, 1.0–1.3 mm; whorls, 4.0–4.5. Protoconch 1.3 whorls, diameter 0.25 mm, initial 0.75 whorl finely wrinkled, later portion smooth except for weak spiral striae. Teleoconch whorls highly convex, shoulders well developed; body whorl often slightly disjunct behind the aperture. Aperture sub-circular, narrowly adnate or, more commonly,

disjunct. Inner lip thin, without columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus perforate. Periostracum tan.

Operculum ovate, light amber, nuclear region dark amber; nucleus eccentric; dorsal surface nearly smooth. Attachment scar thick all around.

Radula 790 × 130 μm, with 63 rows of teeth. Central tooth 19 μm wide, with highly indented dorsal edge; lateral cusps, 4–7; central cusp long, narrow, daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets deep. Lateral tooth formula 3(4)-1-4(5); neck straight; outer wing 230% of cutting edge length. Inner marginal teeth with 20–29 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–32 cusps; cutting edge occupying 22% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum very small.

Cephalic tentacles unpigmented, except for light grey patch proximally, to medium grey-brown. Snout, foot, light to medium grey-brown. Opercular lobe pigment diffuse, light to medium grey, or dark all around. Neck unpigmented, except for scattered granules, to medium grey-brown. Pallial roof, visceral coil dark brown, pigment sometimes uniform. Penial filament and lobe (and small portion of distal penis) darkly pigmented internally; base pigmented with scattered dark granules.

Ctenidial filaments, 11, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland slightly oblique; renal opening grey. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 41A. Albumen gland having very short or no pallial component. Capsule gland as long or longer, but slightly narrower than albumen gland, sub-circular in section; rectal furrow weak. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit mounted on a swollen and weakly raised papilla; anterior extension short. Coiled oviduct a posterior-oblique loop, often kinked at mid-length. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, slightly narrower than albumen gland, ovate-pyriform, longitudinal, with 66% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, proximal portion overlapped by albumen gland, slightly shorter or as long as bursa, narrow to medium width. Seminal receptacle very small, narrow.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having gentle bend. Penis (Figure 41B, C) large; base elongate-rectangular, strongly folded proximally; filament

short, broadly triangular, tapering to point, oblique (angling toward inner edge); lobe slightly shorter than filament, triangular, arising from outer edge of penis, oblique. Ventral gland very small (rarely absent), circular, positioned along inner edge near base. Penial duct straight and near outer edge proximally, bending toward outer edge of filament distally, coursing along edge and terminating at tip of filament.

**Type locality:** Springs, west of Carico Lake, Carico Lake Basin, Lander County, Nevada, T. 26 N, R. 45 E, NW¼ section 16 (Figure 53). Holotype, USNM 874306 (Figure 22E), collected by R. Hershler, 24 July 1991; paratypes, USNM 860693. The type locality consists of two adjacent, thermal (23.5°C.) rheocrenes that feed a small stream. The area is highly impacted by cattle. Snails were collected about 7 m downflow from the spring sources.

**Remarks:** This species is contrasted with *P. basiglans* above.

**Material examined:** NEVADA. *Lander County:* Springs, west of Carico Lake, USNM 860693, USNM 874306.

*Pyrgulopsis pellita* Hershler, sp. nov.

Antelope Valley pyrg

(Figures 9F, 22F, 41D–F)

**Etymology:** From *pellitus* (Latin), covered with skin; referring to the thick periostracum covering the shell of this species.

**Diagnosis:** Medium-sized, with ovate- to narrow-conic shell. Penis large; filament and lobe medium length. Penial ornament a medium-sized terminal gland and large Dg1.

**Description:** Shell (Figures 9F, 22F) ovate- to narrow-conic, apex often eroded, width/height, 70–84%; height, 2.2–3.0 mm; width, 1.7–2.1 mm; whorls, 3.75–4.5. Protoconch 1.4 whorls, diameter 0.38 mm, weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium to high convexity, shoulders weakly developed or absent; sculpture including numerous faint spiral lirae; body whorl often slightly disjunct behind the aperture in largest specimens. Aperture ovate, angled above; adnate or slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus rimate. Periostracum dark red-brown.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 570 × 95 μm, with 62 rows of teeth. Central tooth 29 μm wide, with highly indented dorsal edge; lateral cusps, 6–9; central cusp medium width, daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 4(5)-1-5(6); neck

weakly flexed; outer wing 175% of cutting edge length. Inner marginal teeth with 26–32 cusps; cutting edge occupying 35% of length of tooth. Outer marginal teeth with 37–42 cusps; cutting edge occupying 26% of length of tooth. Stomach slightly longer than style sac; stomach chambers equal-sized; stomach caecum small.

Cephalic tentacles light to medium grey-brown; pigment concentrated proximally. Snout light to medium grey-brown. Foot light grey-brown. Opercular lobe usually dark along inner edge, unpigmented or diffusely pigmented elsewhere. Neck unpigmented, except for scattered grey granules, to medium grey-brown. Pallial roof, visceral coil uniform dark brown-black. Penial filament darkly pigmented internally, lobe and distal penis sometimes pigmented with scattered black granules.

Ctenidial filaments, 16, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, positioned centrally or slightly posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 41D. Albumen gland having very short or no pallial component. Capsule gland as long or slightly longer, but narrower than albumen gland, ovate in section; rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit without anterior extension. Coiled oviduct a tight, posterior-oblique loop preceded by proximal twist or small anterior-oblique bend. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, narrow, narrowly ovate, anterior end weakly distinguished from duct, longitudinal, with 25–50% of length posterior to gland, sometimes slightly overlapped on sides by gland. Bursal duct originating from anterior edge at mid-line and close to oviduct, 50–100% length of bursa, sometimes almost as wide as bursa, usually overlapped proximally (completely or along sides) by albumen gland. Seminal receptacle small, pouchlike, overlapping proximal bursal duct or anteriormost portion of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland small, bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having broad bend. Penis (Figure 41E, F) large; base rectangular, smooth; filament medium length and width, tapering to point, slightly oblique; lobe slightly shorter to slightly longer than filament, cylindrical, longitudinal or slightly oblique. Terminal gland medium-sized, narrow, slightly curved, largely on ventral surface. Dg1 large, rarely greatly reduced, slightly raised, positioned just behind or slightly overlapping base of filament. Ventral penis sometimes bearing raised, glandular dot

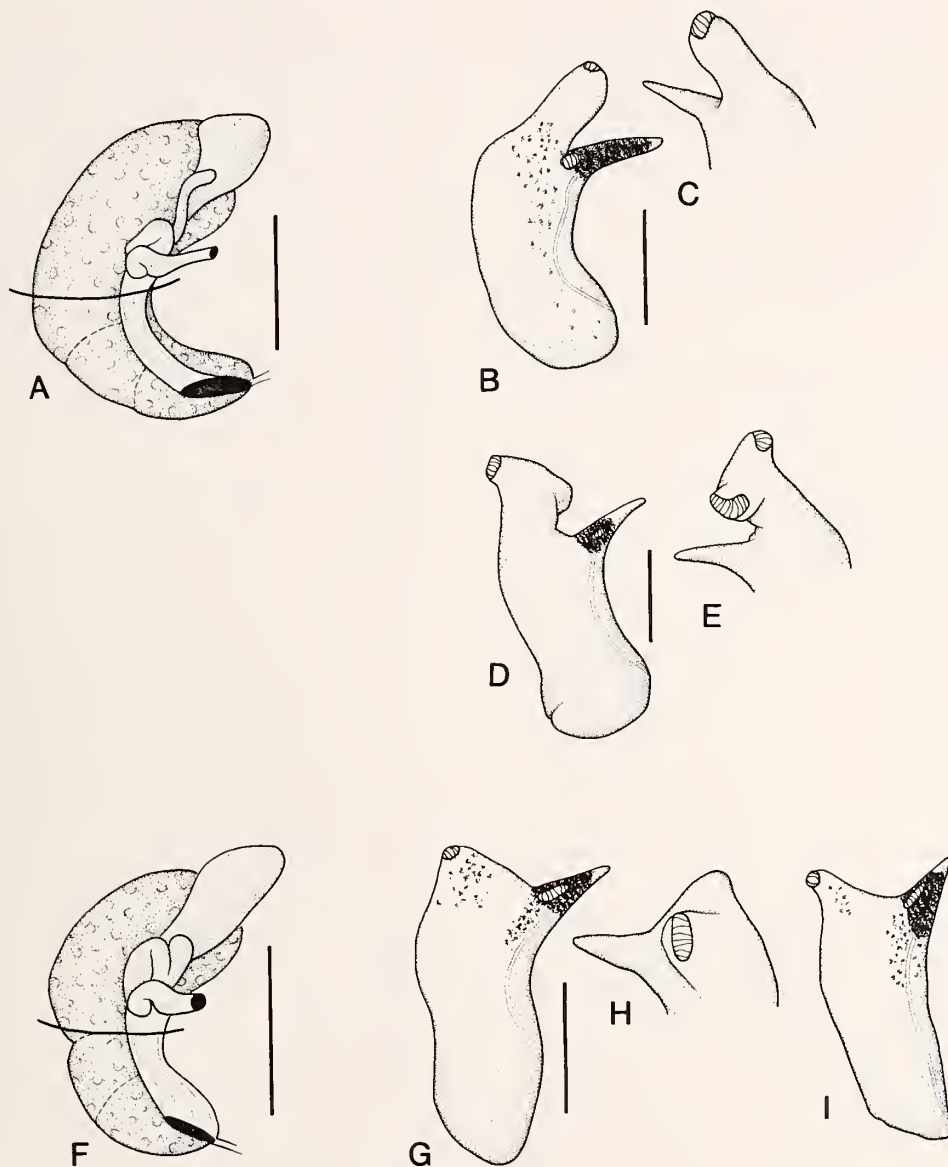


Figure 42

Genitalia of *Pyrgulopsis* species (A–C, *P. leporina*, USNM 860717; D, E, *P. leporina*, USNM 874315; F–I, *P. humboldtensis*, USNM 860718). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two sets of penes (B, C; D, E) are shown for *P. leporina*, and two examples of the dorsal penis (G, I) are shown for *P. humboldtensis*.

alongside base of filament. Penial duct straight, near outer edge.

**Type locality:** Sullivan Spring, Antelope Valley, Eureka County, Nevada, T. 17 N, R. 50 E, NE ¼ section 31 (Figure 53). Holotype, USNM 883850 (Figure 22F), collected by R. Hershler and P. Hovingh, 7 July 1994; paratypes, USNM 860715. The type locality is a small limnocrone

(ca. 2 m wide) surrounded by an old fence. Snails were collected from the pool outflow.

**Remarks:** Among the group of species having penial ornament that includes an elongate Dg1 positioned just behind the penial filament, this species is unique in also having a terminal gland, but no other ornament.

**Material examined:** NEVADA. *Eureka County*: Sullivan Spring, USNM 860715, USNM 874383, USNM 883850.

*Pyrgulopsis leporina* Hershler, sp. nov.

Elko pyrg

(Figures 9G, 22G, 42A–E)

**Etymology:** From *leporinus* (Latin), of hares; referring to location of the type locality in Rabbit Creek drainage, Nevada.

**Diagnosis:** Medium-sized to large, with ovate- to narrow-conic shell. Penis large; filament medium length, lobe short-medium length. Penial ornament a small terminal gland, and very small penial gland.

**Description:** Shell (Figures 9G, 22G) ovate- to narrow-conic, apex often eroded, width/height, 64–78%; height, 3.2–4.8 mm; width, 2.3–3.0 mm; whorls, 3.5–5.25. Protoconch 1.2–1.25 whorls, diameter 0.46 mm, weakly wrinkled at apex and sculptured with faint spiral striae on later portion, otherwise smooth. Teleoconch whorls medium convexity, weakly shouldered; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually slightly disjunct. Inner lip thin, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, without situation. Umbilicus narrowly rimate to perforate. Periostracum tan, covered with thick brown deposit.

Operculum ovate, dark amber-red; nucleus eccentric; dorsal surface weakly frilled; outer margin sometimes having weak rim. Attachment scar thick all around.

Radula  $970 \times 130 \mu\text{m}$ , with 62 rows of teeth. Central tooth  $42 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 4–7; central cusp broad, spoonlike, considerably longer than laterals; basal cusps medium-sized. Basal process broad V-shaped, shorter than lateral margins, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck medium flexed; outer wing 170% of cutting edge length. Inner marginal teeth with 24–27 cusps; cutting edge occupying 31% of length of tooth. Outer marginal teeth with 33–38 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to medium grey-brown, pigmented concentrated proximally. Snout light to medium grey-brown. Foot unpigmented (except for scattered grey granules) to medium grey-brown. Opercular lobe usually dark along inner edge. Neck unpigmented (except for scattered grey granules) to medium grey-brown. Pallial roof, visceral coil dark grey-brown or black, almost uniformly so. Penial filament darkly pigmented internally; dorsal penis otherwise lightly pigmented with scattered grey granules.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly

ovate, centered slightly posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly or not overlapping prostate gland.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 42A. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow absent. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct of two overlapping, posterior-oblique loops. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate-pyriform, anterior portion often poorly distinguished from duct, longitudinal, with 50% of length posterior to gland, sometimes partly overlapped by gland. Bursal duct originating from anterior edge at mid-line, usually at least as long as bursa, medium width, usually lying in depression within albumen gland. Seminal receptacle small, elongate pouch, folded, overlapping anterior portion of bursa or proximal portion of bursal duct.

Testis 2.0 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland small, ovate or bean-shaped, pallial portion very short, narrowly ovate in section. Proximal pallial vas deferens having weak bend or well-developed, reflexed loop. Penis (Figure 42B–E) large; base rectangular, smooth; filament shorter than base, medium width, tapering to point, slightly oblique; lobe slightly longer to slightly shorter than filament, rectangular, often bifurcate distally, longitudinal. Terminal gland small, narrow, often divided into two widely spaced units (with associated bifurcation of distal lobe), rarely trifurcate, transverse, largely on ventral surface. Penial gland very small, restricted to proximal portion of filament, narrower than filament. Dorsal penis sometimes having one to two dotlike units near base of lobe. Small, raised ventral gland seen in one specimen. Penial duct straight, near outer edge.

**Type locality:** Springs, Rabbit Creek, Humboldt River drainage, Elko County, Nevada, T. 33 N, R. 57 E, SE  $\frac{1}{4}$  section 2. Holotype, USNM 874336 (Figure 22G), collected by R. Hershler, 30 July 1991; paratypes, USNM 860717. The type locality is a shallow, moderately broad (7 m) helocrene slightly impacted by cattle.

**Remarks:** This species most closely resembles *P. serrata*, from Steptoe Valley, with which it shares penial ornament of small penial and terminal glands. *Pyrgulopsis leporina* differs from the above in its much larger central radular teeth, spoon-shaped central cusps on these teeth, larger penial lobe, and larger bursa copulatrix. The distribution of this snail is shown in Figure 53.

**Material examined:** NEVADA. *Elko County*: Springs,



Rabbitt Creek, USNM 860717, USNM 874336.—Persons Spring, Ruby Valley, T. 34 N, R. 60 E, NW ¼ section 26, USNM 874315.

*Pyrgulopsis humboldtensis* Hershler, sp. nov.

Humboldt pyrg

(Figures 9H, 13E, 22H–J, 42F–I)

**Etymology:** Referring to distribution of this species in Humboldt River drainage, Nevada.

**Diagnosis:** Medium-sized, with sub-globose to ovate-conic shell. Penis large; filament and lobe short. Penial ornament a small terminal gland, very small penial gland, and medium-sized ventral gland.

**Description:** Shell (Figures 9H, 22H–J) sub-globose to ovate-conic, width/height, 70–91%; height, 2.0–3.1 mm; width, 1.7–2.3 mm; whorls, 3.75–4.5. Protoconch 1.3–1.4 whorls, diameter 0.40 mm, initial 0.5–0.75 whorl weakly wrinkled (mostly along inner edge), otherwise smooth. Teleoconch whorls highly convex, broadly shouldered; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip complete, thin, without columellar shelf. Outer lip thin, weakly prosocline, without sinuation. Umbilicus perforate. Periostracum brown.

Operculum (Figure 13E) ovate, dark amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 760 × 125 μm, with 54 rows of teeth. Central tooth 31 μm wide, with highly indented dorsal edge; lateral cusps, 5–6; central cusp narrow to medium width, daggerlike, basal cusps small, sometimes accompanied by thickening to outside. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck straight or weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 19–21 cusps; cutting edge occupying 32% of length of tooth. Outer marginal teeth with 28–32 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout light to medium grey-brown. Foot medium to dark grey-brown. Opercular lobe dark along inner edge, sometimes all around. Neck light to medium grey. Pallial roof, visceral coil dark brown-black, pigment sometimes uniformly dark. Proximal 67% of penial filament darkly pigmented; distal penis and lobe often medium-darkly pigmented.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrowly ovate, centered slightly posterior to middle of ctenidium. Renal gland strongly oblique; kidney opening slightly thickened. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior

stomach chamber. Distal female genitalia shown in Figure 42F. Albumen gland having very short or no pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop preceded by small, posterior-oblique twist. Oviduct and bursal duct joining slightly behind pallial wall. Bursa copulatrix slightly shorter than albumen gland, medium width, narrowly ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, very short, narrow-medium width. Seminal receptacle small, pouchlike, overlapping or ventral to anterior portion of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 42G–I) large; base rectangular, very weakly folded or smooth; filament short, narrow, tapering to point, oblique; lobe usually slightly longer than filament, knoblike or broadly triangular (tapering), strongly oblique. Terminal gland small, sub-circular, usually dorsal. Penial gland filling 25–50% of filament, narrow, positioned near inner edge. Dot-like gland positioned near outer edge medially (corresponding to Dg1) seen in one specimen. Ventral gland medium-sized, ovate, borne on prominent swelling, longitudinal, positioned alongside base of filament. Penial duct straight, near outer edge.

**Type locality:** Springs, East Fork Beaver Creek (above confluence of Cabin Creek), North Fork Humboldt River, Elko County, Nevada, T. 41 N, R. 57 E, SE ¼ section 27. Holotype, USNM 874722 (Figure 22H), collected by R. Hershler and P. Hovingh, 28 August, 1992; paratypes, USNM 860718. The type locality is a shallow, 8 m wide helocrene moderately impacted by cattle.

**Remarks:** This snail is contrasted with *P. pictilis*, from Antelope Valley (Lander County), above. *Pyrgulopsis humboldtensis* is also closely similar to some populations of widespread *P. kolobensis*, but differs in its broader shell, more pointed central cusps on the central radular teeth, more elongate outer wings on the lateral radular teeth, and smaller penial lobe with weaker terminal gland. The distribution of this species is shown in Figure 53.

**Material examined:** NEVADA. *Elko County:* Springs, East Fork Beaver Creek, T. 41 N, R. 57 E, SE ¼ section 27, USNM 860718, USNM 874722.—Springs, Hot Springs Creek, Marys River drainage, T. 39 N, R. 59 E, NW ¼ section 5, USNM 874725.—Springs, South Fork Hanks Creek, Marys River drainage, T. 40 N, R. 59 E, SW ¼ section 19, USNM 874719.—Spring, Marys River drainage, T. 39 N, R. 59 E, section 1, USNM 854544.

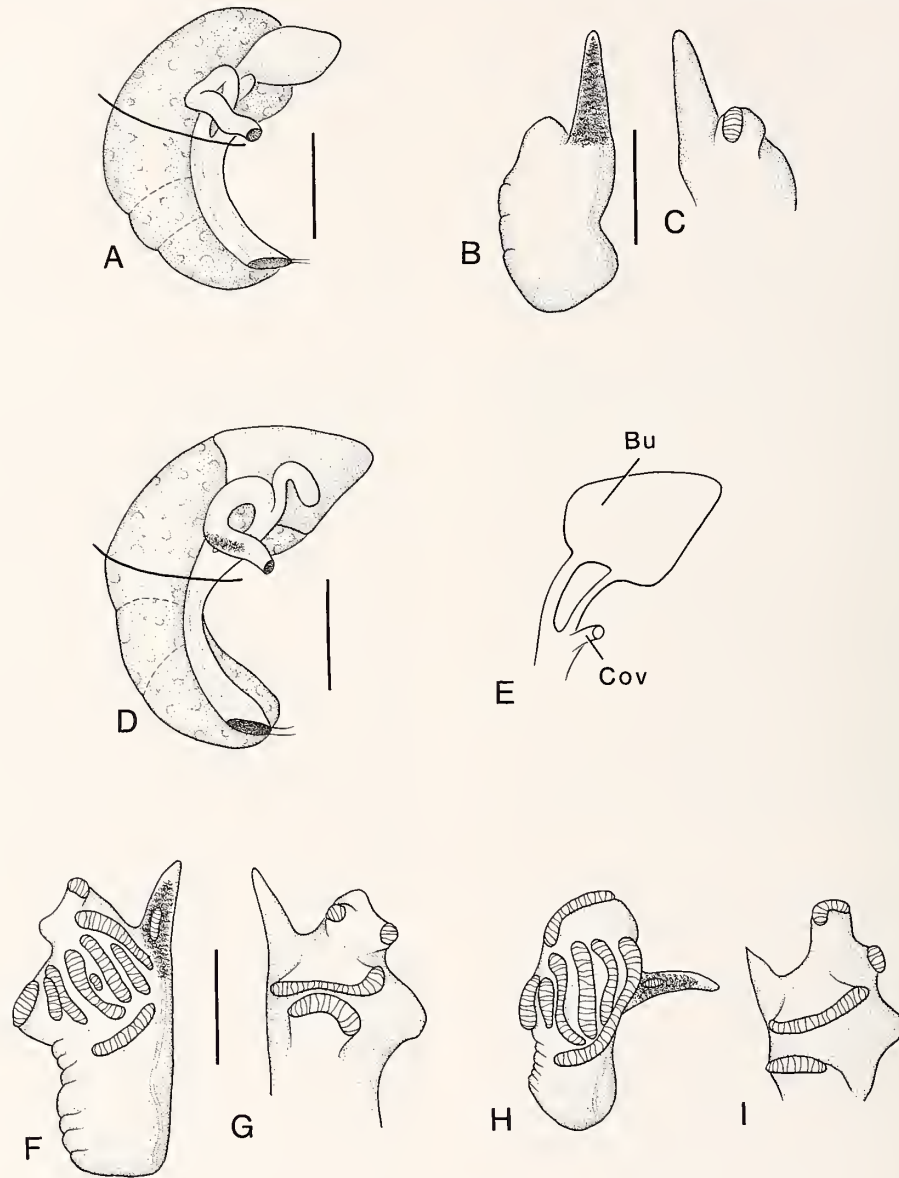


Figure 43

Genitalia of *Pyrgulopsis* species (A–C, *P. hamlinensis*, USNM 860695; D–G, *P. peculiaris*, USNM 883602; H, *P. peculiaris*, USNM 883603; I, *P. peculiaris*, USNM 874766). A. Female glandular oviduct and associated structures, bar = 0.25 mm. B. Dorsal aspect of penis, bar = 0.25 mm. C. Ventral aspect of distal penis, scale as in B. D. Female glandular oviduct and associated structures, bar = 0.25 mm. E. Bursa copulatrix and bifid duct, scale as in D. F. Dorsal aspect of penis, bar = 0.5 mm. G. Ventral aspect of distal penis, scale as in F. H. Dorsal aspect of penis, scale as in F. I. Ventral aspect of distal penis, scale as in F. A–E. Bars = 0.25 mm. F–I. Bars = 0.5 mm. Bu = bursa copulatrix, Cov = coiled oviduct.

### Species from the Oregon Lakes

#### *Pyrgulopsis hendersoni* (Pilsbry, 1933)

*Amnicola hendersoni* Pilsbry, 1933, pl. 2: figs 2, 9, 10.

*Fontlicella hendersoni* (Pilsbry, 1933), Taylor, 1975:94–95 [literature compilation].

*Fontlicella hendersoni* (Pilsbry, 1933), Taylor & Smith, 1981:351–352 [locality records].

*Pyrgulopsis hendersoni* (Pilsbry, 1933), Hershler & Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Hershler, 1994:39, 41 [figures].

**Diagnosis:** Large, with ovate to low-conical shell. Penis

large, filament short, lobe medium length. Penial ornament a large terminal gland, large Dg1, small Dg2, small Dg3, and small ventral gland.

**Type locality:** South of Burns, Oregon.

**Remarks:** The Abert Lake Basin population (Figure 53), although disjunct from the previously known range of *P. hendersoni* (Harney Lake and Malheur River basins to the northeast), closely conforms to this species, differing principally in having a smaller ventral gland on the penis. The large-snail collected by Taylor & Smith (1981:352; *F[ontelicella]*, sp.) from near the north end of Lake Abert also may be referable to this species.

**Material examined:** OREGON. *Lake County:* Springs, northwest corner Lake Abert, T. 33 S, R. 21 E, SW ¼ section 16, USNM 883547.

### *Pyrgulopsis intermedia* (Tryon, 1865)

- Pomatiopsis intermedia* Tryon, 1865, 1865, pl. 22, fig. 8.  
*Fontelicella intermedia* (Tryon, 1865), Taylor, 1975: 104 [literature compilation].—Taylor, 1985:308–310.  
*Pyrgulopsis intermedia* (Tryon, 1865), Hershler & Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Hershler, 1994:42, 44 [figures].

**Diagnosis:** Large, with ovate-conic shell. Penis medium-sized, filament and lobe medium length. Penial ornament a large terminal gland, medium-sized penial gland, and large ventral gland.

**Type locality:** Owyhee River, southeast Oregon.

**Remarks:** Taylor (1985) earlier noted on the occurrence of this snail in Barren Valley (Figure 53), a small endorheic drainage positioned between South Fork Malheur River and Owyhee River. Barren Valley populations closely resemble snails from the type locality area, but are slightly smaller and have squatter shells.

**Material examined:** OREGON. *Malheur County:* Sky-light Spring, Barren Valley, T. 28 S, R. 38 E, SW ¼ section 8, USNM 854126.—Spring, Dowell Ranch, Barren Valley, T. 27 S, R. 38 E, SW ¼ section 33, USNM 874179.

## Species from the Bonneville Basin

### *Pyrgulopsis kolobensis* (Taylor, 1987)

- Paludestrina longinqua* (Gould, 1855), Pilsbry, 1899:122 [not Gould, 1855; in part].—Hannibal, 1912a:34 [in part].—Hannibal, 1912b:186 [in part].—Henderson & Daniels, 1916:322, 334 [in part].—Henderson & Daniels, 1917:64, 71, 72, 76.—Henderson, 1924:190.—Chamberlin & Jones, 1929:176–178, fig. 82 [in part].—Berry, 1931:114.—Jones, 1935:228 [in part?].—Jones, 1940a:42 [in part].—Jones, 1940b:29 [in part].—Woolstenhulme, 1942a:14 [in part].—Woolstenhulme, 1942b:55 [in part].

- Amnicola (Cincinnati) cincinnatiensis* (Anthony, 1840), Henderson, 1924:190 [not Anthony, 1840].  
*Cincinnati cincinnatiensis* (Anthony, 1840), Chamberlin & Jones, 1929:175–176 [not Anthony, 1840].  
*Amnicola longinqua* Gould, 1855, Call, 1884:20–21 [not Gould, 1855; in part].—Henderson, 1936:137 [in part].—Chamberlin & Roscoe, 1948:11.—E.G. Berry, 1948:69.  
*Fontelicella longinqua* (Gould, 1855), Russell, 1971:232–233, fig. 4 (penis) [not Gould, 1855].  
*Fontelicella kolobensis* Taylor, 1987:19, fig. 8.  
*Fontelicella pinetorum* Taylor, 1987:20, fig. 9.—Hershler, 1994 [placed in synonymy with *Pyrgulopsis kolobensis*].  
*Pyrgulopsis kolobensis* (Taylor, 1987), Hershler, 1994:44, 46 [figures; transfer to *Pyrgulopsis*].

**Diagnosis:** Medium-sized to large, shell usually ovate-conic. Penis large, filament short, lobe medium-long. Penial ornament variable, but typically a large terminal gland, small penial gland, and large ventral gland.

**Type locality:** Toquerville Springs, Washington County, Utah, T. 40 S, R. 13 W, section 35.

**Remarks:** This species (and its junior synonym, *Fontelicella pinetorum*) had been previously recorded only from the upper Virgin River basin in southwest Utah. However, *Pyrgulopsis kolobensis* is clearly conspecific with the widespread snail of the eastern Great Basin, which is found as far south as the northern flank of the mountain range composing the Great Basin-Virgin River divide, and which has been identified as *Paludestrina longinqua* Gould, 1855 in the literature. As explained elsewhere (Hershler, 1994:47), *Pyrgulopsis longinqua* (Gould, 1855) is restricted to its type locality area in the Salton Trough of southern California and, although these two species share some presumably derived penial features, they do not appear to be closely related (Hershler, 1994, fig. 31).

The range of *P. kolobensis* is herein extended to include much of the Bonneville Basin (including the Sevier River sub-basin and a few localities from both upper and lower Bear River drainage), as well as various isolated drainages of eastern Nevada and portions of the Colorado River basin (Meadow Valley Wash in southern Nevada, Strawberry River drainage in the Wasatch Mountains of Utah) (Figure 54).

Variation is considerable within this broadly distributed species. Although typically ovate-conic, the shell also may be either broadly conical (such as in populations from southern Steptoe Valley) or narrow-conic (Independence Valley). The terminal gland of the penis is usually fairly large and curved, but may also be short, and either ovate or (rarely) circular. The penial gland often is small (and is absent in one population from the Virgin River drainage) and confined to the base of the filament, but also may be long, filling most of the filament and often extending a short or long distance onto the base. In some populations the penial gland appears to be split and/or

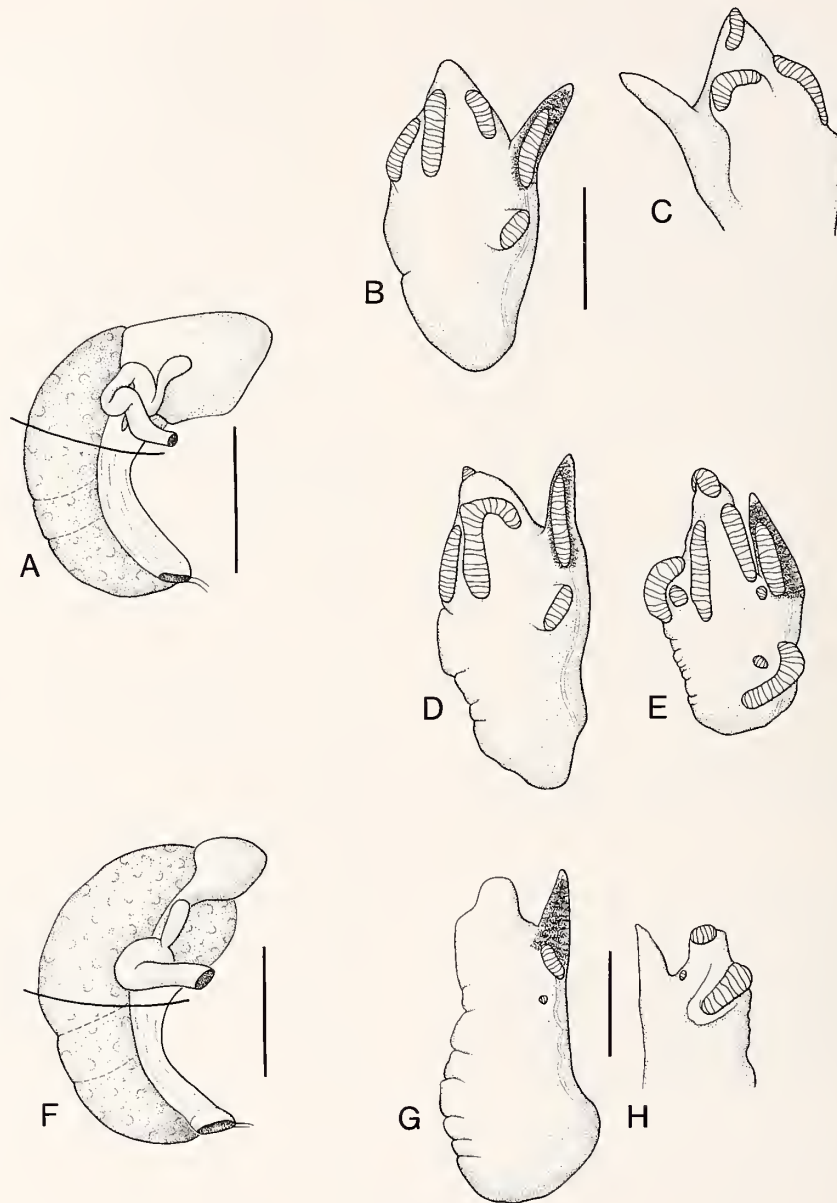


Figure 44

Genitalia of *Pyrgulopsis* species (A–E, *P. anguina*, USNM 860725; F–H, *P. saxatilis*, USNM 860726). A–E. Bars = 0.5 mm. F–H. Bars = 0.25 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two sets of penes (B, C; D, E) are shown for *P. anguina*.

accompanied by a more proximal, longitudinal Dg1. In many populations Dg1 is well developed, and may be raised on a pedicel and/or have a decidedly transverse orientation. A Dg2 often is present as a narrow, distal unit (sometimes raised). A proximal gland, also found along the inner edge, may also be present (notably in populations from Huntington, Newark, and Ruby Valleys), either instead of or in addition to the typical Dg2.

In a few populations, the ventral gland is multiple (Mound Valley). Penial variation can be considerable even within a single population or among those of a small drainage and unusual forms are linked with typical morphology by intermediates in all cases, hence I choose not to sub-divide this taxon at this time.

**Material examined:** IDAHO. *Bannock County*: Heart

Mountain Spring (outflow), Stockton Creek, Bear River drainage, T. 13 S, R. 39 E, NW ¼ section 6, USNM 883681.—Spring, north of road along Stockton Creek, Bear River drainage, T. 13 S, R. 39 E, NW ¼ section 6, USNM 883691.—Stockton Creek, Bear River drainage, T. 13 S, R. 39 E, NW ¼ section 6, USNM 883536, USNM 883894. *Franklin County*: Spring, upper Cub River, Bear River drainage, T. 15 S, R. 41 E, NW ¼ section 8, USNM 874697, USNM 883568. *Oneida County*: Big Malad Spring, Malad Valley, T. 14 S, R. 35 E, NW ¼ section 10, USNM 883480.—Twin Springs, Curlew Valley, T. 13 S, R. 32 E, NW ¼ section 30, USNM 883595.—Springs, southeast of Stone Reservoir, Curlew Valley, T. 16 S, R. 33 E, NW ¼ section 7, USNM 883390. *NEVADA. Elko County*: Springs, north-northwest Denton Canyon, Butte Valley, T. 28 N, R. 62 E, SW ¼ section 3, USNM 874308.—Spring, north-northwest of The Narrows, Butte Valley, T. 28 N, R. 61 E, SW ¼ section 36, USNM 874283.—Springs, Toyn Creek, Mound Valley, T. 28 N, R. 57 E, SW ¼ section 5, USNM 874339.—Spring, Toyn Creek, Mound Valley, T. 28 N, R. 57 E, NW ¼ section 10, USNM 874257.—Spring, southwest side of North Sump, Ruby Valley, T. 27 N, R. 58 E, SW ¼ section 18, USNM 873337, USNM 874316.—Spring, southwest side of North Sump, Ruby Valley, T. 27 N, R. 58 E, section 7, USNM 873341.—Spring, southeast side of North Sump, Ruby Valley, T. 27 N, R. 58 E, SW ¼ section 10, USNM 873328, USNM 874282.—Spring, southeast side of North Sump, Ruby Valley, T. 27 N, R. 58 E, NE ¼ section 16, USNM 873338.—Gamble Spring, Thousand Springs Creek, T. 40 N, R. 69 E, NW ¼ section 8, USNM 874717.—Hellman Spring, Huntington Valley, T. 27 N, R. 55 E, NE ¼ section 36, USNM 874078, USNM 874337.—Springs, South Fork Twin Creek, Huntington Valley, T. 27 N, R. 56 E, SE ¼ section 6, USNM 874071, USNM 874317, USNM 874674.—Big Springs, Independence Valley, T. 36 N, R. 66 E, NE ¼ section 33, USNM 874330. *Eureka County*: upper Huntington Creek, Huntington Valley, T. 25 N, R. 55 E, NW ¼ section 35, USNM 874333.—upper Huntington Creek, Huntington Valley, T. 25 N, R. 55 E, SE ¼ section 34, USNM 873336.—Spring, upper Huntington Creek, Huntington Valley, T. 25 N, R. 55 E, SE ¼ section 34, USNM 873410.—Fish Creek Springs, Fish Creek Valley, T. 16 N, R. 53 E, NW ¼ section 8, USNM 874764, USNM 874875.—Simpson Springs, Diamond Valley, T. 19 N, R. 54 E, NW ¼ section 22, USNM 874324.—Springs, Roberts Creek, Kobeh Valley, T. 23 N, R. 50 E, NE ¼ section 35, USNM 874334.—Pratt Springs, Pine Valley, T. 27 N, R. 52 E, SE ¼ section 10, USNM 874301.—Tonkin Spring, Denay Valley, T. 23½ N, R. 49 E, SW ¼ section 1, USNM 874313, USNM 874716.—Hand-Me-Down Creek, Crescent Valley, T. 28 N, R. 49 E, SE ¼ section 3, USNM 874302. *Lincoln County*: Spring, Kershaw-Ryan State Park, Meadow Valley Wash, T. 4 S, R. 67 E, NE ¼ section 19, USNM 854170, USNM 873184, USNM

873455, USNM 874039, USNM 874761.—North Spring, Clover Valley, Meadow Valley Wash, T. 5 S, R. 69 E, SW ¼ section 11, USNM 874768.—Spring, Spring Valley State Park, Meadow Valley Wash, T. 2 N, R. 70 E, NE ¼ section 7, USNM 874675, USNM 874777.—Spring, west-northwest of Cottonwood Wash, Spring Valley, Meadow Valley Wash, T. 2 N, R. 70 E, NW ¼ section 5, USNM 874679, USNM 874766. *Nye County*: Butterfield Springs, White River Valley, T. 7 N, R. 57 E, NE ¼ section 28, USNM 873155.—Springs below Black Spring, Sand Creek, Garden Valley, T. 3 N, R. 57 E, NW ¼ section 27, USNM 874661.—Butterfield Springs, Railroad Valley, T. 8 N, R. 57 E, SE ¼ section 27, USNM 873155.—Thorn Spring (north), Railroad Valley, T. 7 N, R. 57 E, SW ¼ section 28, USNM 883854.—Thorn Spring, Railroad Valley, T. 7 N, R. 57 E, section 28, USNM 874087.—Spring, Troy Canyon, Railroad Valley, T. 6 N, R. 57 E, SW ¼ section 28, USNM 883845.—Stream, Troy Canyon, Railroad Valley, T. 6 N, R. 57 E, NE ¼ section 34, USNM 883247.—Spring, northeast of Tom Spring, Railroad Valley, T. 8 N, R. 57 E, SW ¼ section 1, USNM 873169.—Springs, ca. 2.4 km north-northwest of Currant, Railroad Valley, T. 11 N, R. 58 E, NW ¼ section 32, USNM 873171.—Spring, south of Cottonwood Canyon, Reveille Valley, T. 2 N, R. 50 E, NE ¼ section 28, USNM 883546. *White Pine County*: Spring, Snake Creek, Snake Valley, T. 12 N, R. 70 E, NW ¼ section 17, USNM 874670.—Spring, Snake Creek, Snake Valley, T. 12 N, R. 70 E, section 16, USNM 873430.—Willow Patch Spring, Snake Valley, T. 15 N, R. 68 E, SE ¼ section 36, USNM 854169, USNM 874281, USNM 874669.—Spring, southwest of Caine Spring, Snake Valley, T. 15 N, R. 17 E, NE ¼ section 31, USNM 874277.—Spring, Minerva, Spring Valley, T. 11 N, R. 67 E, SE ¼ section 12, USNM 874668.—Spring, 1.6 km north of Minerva, Spring Valley, T. 11 N, R. 67 E, SW ¼ section 1, USNM 874665.—Spring, 3.2 km north of Minerva, Spring Valley, T. 12 N, R. 67 E, NW ¼ section 36, USNM 873217, USNM 874676.—Springs, southeast of Cleve Creek, Spring Valley, T. 16 N, R. 67 E, SW ¼ section 32, USNM 874332.—Springs, southeast of Cleve Creek, Spring Valley, T. 16 N, R. 67 E, NE section 32, USNM 873229.—Springs, southeast of Cleve Creek (0.3 km east of above), Spring Valley, T. 16 N, R. 67 E, NE section 32, USNM 873199.—Spring, lower Cleve Creek, Spring Valley, T. 16 N, R. 67 E, SW ¼ section 20, USNM 873225.—Springs, Stonehouse, Spring Valley, T. 22 N, R. 66 E, SW ¼ section 17, USNM 874309.—Cane Spring, Pleasant Valley, T. 21 N, R. 70 E, SW ¼ section 22, USNM 874279.—Lower Sanford Spring, Deep Creek Valley, T. 23 N, R. 69 E, NE ¼ section 25, USNM 874274.—Springs, West Deep Creek, Deep Creek Valley, T. 24 N, R. 70 E, NE ¼ section 3, USNM 874278.—Tippett Springs, Antelope Valley, T. 23 N, R. 67 E, NW ¼ section 14, USNM 874338, USNM 883592.—Chin Creek, Antelope Valley, T. 25 N, R. 67 E, NE ¼ section

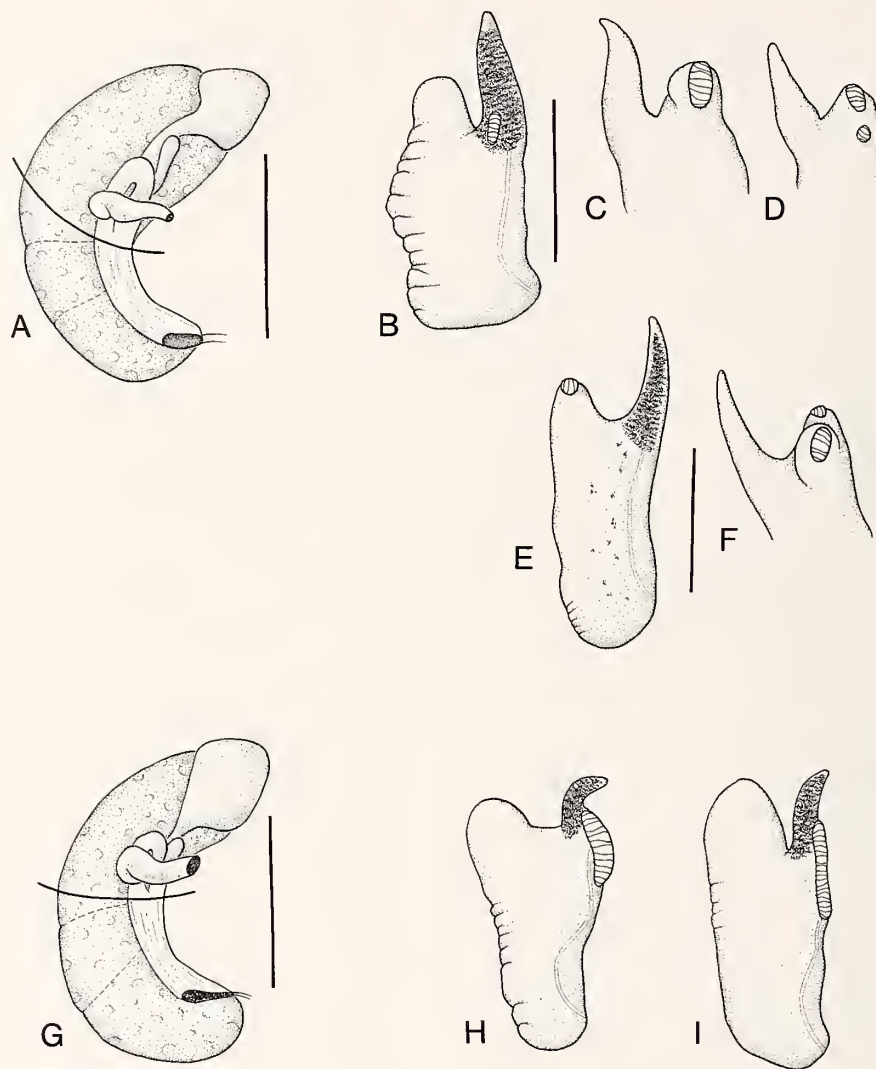


Figure 45

Genitalia of *Pyrgulopsis* species (A–D, *P. variegata*, USNM 860723; E, F, *P. variegata*, USNM 883599; G–I, *P. hovinghi*, USNM 874715). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. hovinghi*, which lacks ventral ornament). Two sets of penes (B, C; E, F) and a third example of the ventral penis (D) are shown for *P. variegata*.

26, USNM 874323.—Spring, west side HWY 318, ca. 9.6 km south of Lund, White River Valley, T. 11 N, R. 62 E, USNM 873161.—Spring, west side HWY 6, west-northwest of Preston, White River Valley, T. 13 N, R. 61 E, SW  $\frac{1}{4}$  section 31, USNM 873330, USNM 874680.—Spring, Bull Creek, Railroad Valley, T. 14 N, R. 56 E, SE  $\frac{1}{4}$  section 14, USNM 874774, USNM 874881.—Green Springs, Railroad Valley, T. 15 N, R. 57 E, SW  $\frac{1}{4}$  section 33, USNM 874773, USNM 874874.—Bennett Spring, Steptoe Valley, T. 19 N, R. 63 E, SE  $\frac{1}{4}$  section 33, USNM 874303.—Springs, northwest of Clark Spring,

Steptoe Valley, T. 19 N, R. 63 E, NE  $\frac{1}{4}$  section 32, USNM 873220.—Springs, northwest of Clark Spring, Steptoe Valley, T. 19 N, R. 63 E, NW  $\frac{1}{4}$  section 20, USNM 874691, USNM 883937.—Springs, Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW  $\frac{1}{4}$  section 5, USNM 892017.—Springs, Steptoe Ranch, Steptoe Valley, T. 19 N, R. 63 E, NW  $\frac{1}{4}$  section 5, USNM 873221.—Spring, north of Steptoe Ranch, Steptoe Valley, White Pine County, Nevada, T. 19 N, R. 63 E, SW  $\frac{1}{4}$  section 5, USNM 873206.—Spring, Schell Creek, Steptoe Valley, T. 22 N, R. 65 E, NE  $\frac{1}{4}$  section 7,

USNM 874325.—Springs, Schell Creek, ca. 1 km below Schellbourne Pass, Steptoe Valley, T. 22 N, R. 65 E, SE ¼ section 5, USNM 873236.—Owens Springs, Butte Valley, T. 26 N, R. 62 E, NW ¼ section 33, USNM 874321.—Springs, southwest side of Newark Lake, Newark Valley, T. 20 N, R. 55 E, sections 4, 5, 8, USNM 873332.—Minoletti Spring, Newark Valley, T. 22 N, R. 55 E, NW ¼ section 11, USNM 874328.—Cold Spring, Newark Valley, T. 23 N, R. 55 E, NW ¼ section 26, USNM 874320, USNM 874901.—Station Spring, Ruby Valley, T. 25 N, R. 57 E, NE ¼ section 13, USNM 874311.—Narcise Springs, Ruby Valley, T. 25 N, R. 57 E, SW ¼ section 2, USNM 874307.—Springs, northwest of Narcise Springs, Ruby Valley, T. 25 N, R. 57 E, NE ¼ section 3, USNM 873335. UTAH. *Box Elder County*: Blue Creek Spring, Blue Creek Valley, T. 13 N, R. 5 W, NW ¼ section 29, USNM 883625.—Spring, ca. 3.5 km east-northeast of Portage, Malad Valley, T. 15 N, R. 3 W, NE ¼ section 4, USNM 883490, USNM 883577.—Spring, ca. 1.6 km north of Promontory Point, Promontory Mountains, Great Salt Lake Desert, T. 6 N, R. 5 W, NE ¼ section 21, USNM 883611.—Shaw Spring, Promontory Mountains, Great Salt Lake Desert, T. 7 N, R. 5 W, NE ¼ section 9, USNM 883607.—Springs, ca. 1.6 km south of Sweetwater Spring, Promontory Mountains, Great Salt Lake Desert, T. 8 N, R. 5 W, center section 5, USNM 883632.—Spring, east of Rozel Flat, Promontory Mountains, Great Salt Lake Desert, T. 9 N, R. 6 W, NE ¼ section 31, USNM 854782.—Spring, ca. 0.8 km north of Mantua Reservoir, Great Salt Lake Desert, T. 9 N, R. 1 W, NE ¼ section 16, USNM 883569.—Salt Spring, Point Lookout, Salt Creek, Great Salt Lake Desert (Figure 5C), T. 11 N, R. 3 W, SE ¼ section 6, USNM 874067, USNM 883216.—Spring, Painted Rock, Salt Creek, Great Salt Lake Desert, T. 10 N, R. 4 W, NW ¼ section 11, USNM 883209, USNM 883399.—Spring, Jesses Knoll, Salt Creek, Great Salt Lake Desert, T. 11 N, R. 4 W, SE ¼ section 34, USNM 874069, USNM 883234, USNM 883400.—Springs, west-southwest of Connor Springs, Salt Creek, Great Salt Lake Desert, T. 10 N, R. 5 W, NW ¼ section 12, USNM 883198, USNM 883401.—Spring, southwest of Lampo Junction, Great Salt Lake Desert, T. 10 N, R. 5 W, NE ¼ section 4, USNM 854548, USNM 883388.—Bar M Spring, Great Salt Lake Desert (Figure 5B), T. 11 N, R. 10 W, SE ¼ section 1, USNM 883630.—Spring, east side HWY 30, west of Dove Creek Hills, Great Salt Lake Desert, T. 11 N, R. 15 W, NW ¼ section 14, USNM 883615.—So. Tremonton, FMNH 178357.—Spring, north of Plymouth, Malad Valley, FMNH 224314. *Cache County*: Spring, below (west of) Porcupine Reservoir, Cache Valley, T. 9 N, R. 2 E, NW ¼ section 17, USNM 883853.—Pool alongside Logan River, Logan Canyon, Cache Valley, T. 12 N, R. 2 E, NW ¼ section 27, USNM 883575.—Spring, Spring Hollow, Logan Canyon, Cache Valley, T. 12 N, R. 2 E, NW ¼ section 27, USNM 858290.—Murray Spring;

Cache Valley, T. 10 N, R. 1 W, SW ¼ section 10, USNM 883476. *Davis County*: Spring, ca. 1.6 km northeast of Mushroom Spring, Antelope Island, Great Salt Lake Desert, T. 2 N, R. 3 W, NW ¼ section 11, USNM 883219, USNM 883489. *Iron County*: Spring, east of Summit, Parowan Valley, T. 34 S, R. 9 W, SE ¼ section 31, USNM 883612.—Spring, upper Little Creek, Parowan Valley, T. 34 S, R. 7 W, NE ¼ section 17, USNM 883616.—Kane Spring, Parowan Valley, T. 32 S, R. 9 W, NE ¼ section 12, USNM 883593.—Spring, Upper Bear Valley, T. 33 S, R. 7 W, NE ¼ section 23, USNM 883619.—West Spring, Lower Bear Valley, T. 32 S, R. 6 W, SW ¼ section 28, USNM 883589.—Big Swamp Springs, Lower Bear Valley, T. 32 S, R. 6 W, NW ¼ section 23, USNM 883601. *Juab County*: Springs, McIntyre, Tintic Valley, T. 11 S, R. 3 W, SE ¼ section 28, USNM 883206.—Baker Hot Springs, Old River Bed, T. 14 S, R. 8 W, SE ¼ section 10, USNM 883238, USNM 883431.—Cherry Creek, below Indian Springs, Old River Bed, T. 12 S, R. 5 W, NW ¼ section 21, USNM 883197.—Spring, Mount Laird, Sevier Desert, T. 14 S, R. 11 W, center section 26, USNM 883226, USNM 883432.—Spring, northeast of Chicken Creek Reservoir, Juab Valley, T. 15 S, R. 1 W, NE ¼ section 16, USNM 883426, USNM 883438.—Springs, Hollow Creek, Juab Valley, T. 13 S, R. 2 E, NW ¼ section 5, USNM 883600.—Springs, Curiant Creek, Juab Valley, T. 12 S, R. 1 E, NW ¼ section 18, USNM 883195.—Spring, Mona, Juab Valley, T. 11 S, R. 1 E, NE ¼ section 31, USNM 874077, USNM 883240.—Spring, south of Starr, Juab Valley, T. 11 S, R. 1 E, SW ¼ section 8, USNM 874070, USNM 874072, USNM 883231.—“Percy Spring,” south end Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, SE ¼ section 26, USNM 858289, USNM 883473.—Spring, near south end Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, NE ¼ section 26, USNM 858280.—Spring, southwest of “Mallard Pool,” Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, NE ¼ section 23, USNM 883200.—North Springs, Fish Springs National Wildlife Refuge, Great Salt Lake Desert, T. 11 S, R. 14 W, SE ¼ section 3, USNM 883217.—“Leland Harris” Springs, Snake Valley, T. 14 S, R. 18 W, NE ¼ section 32, USNM 883223.—Spring (source), Spring Creek, Deep Creek Valley, T. 11 S, R. 19 W, SW ¼ section 19, USNM 874276. *Millard County*: Coyote Spring, Beaver River drainage, T. 23 S, R. 9 W, NW ¼ section 33, USNM 883239.—Tie House Spring, Beaver River drainage, T. 24 S, R. 10 W, NE ¼ section 22, USNM 883212.—Spring Lake (Clear Lake), Sevier River drainage, T. 20 S, R. 7 W, NW ¼ section 11, USNM 883214.—Painter Spring, Tule Valley, T. 19 S, R. 14 W, NE ¼ section 5, USNM 883202.—Sinbad Spring, Tule Valley, T. 16 S, R. 13 W, NE ¼ section 33, USNM 883207, USNM 883424.—Spring, at corral, east of Horse Canyon, Snake Valley, T. 17 S, R. 19 W, NE ¼ section 29, USNM 883220.—Knoll

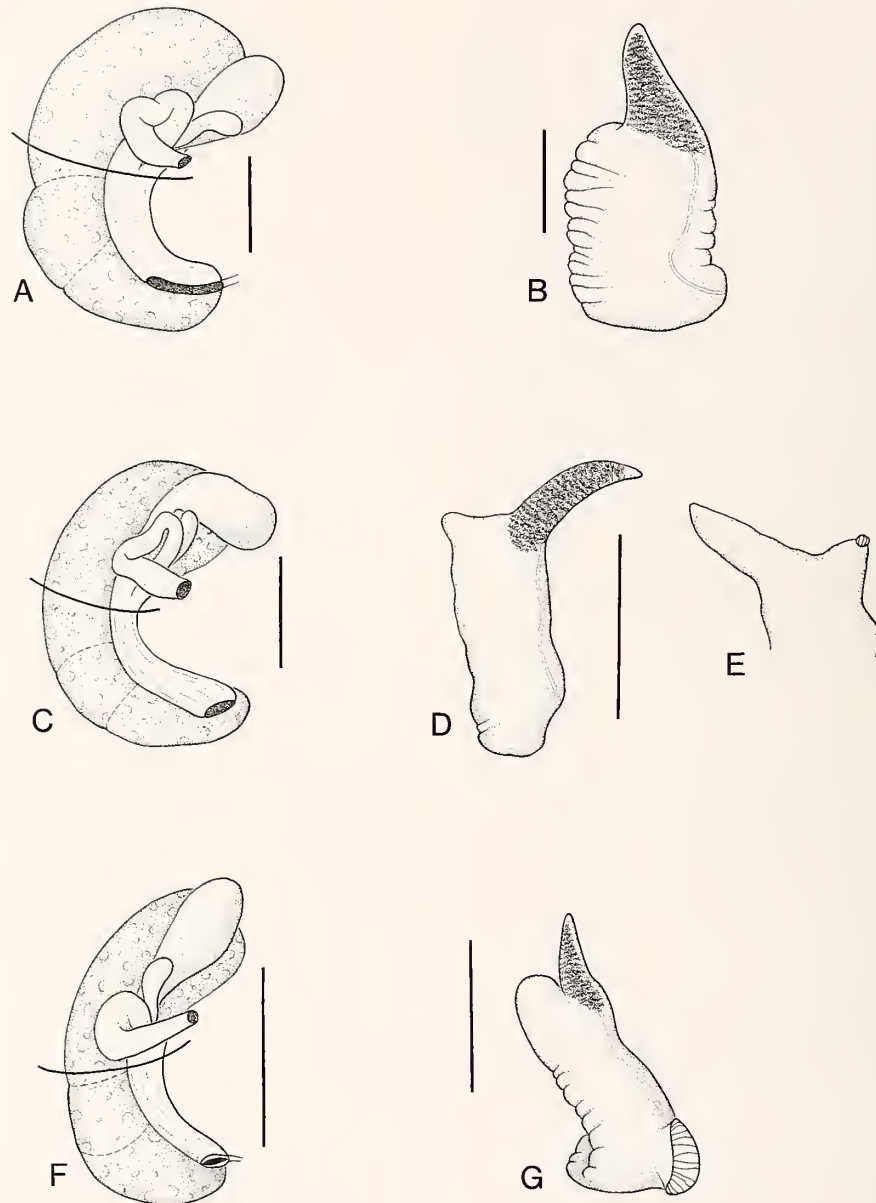


Figure 46

Genitalia of *Pyrgulopsis* species (A, B, *P. millenaria*, USNM 860721; C-E, *P. lentiglans*, USNM 860722; F, G, *P. plicata*, USNM 860727). A, B, Bars = 0.25 mm. C-G, Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis (not shown for *P. millenaria* and *P. lentiglans*, which lack ventral ornament).

Springs, Snake Valley, T. 18 S, R. 18 W, NE  $\frac{1}{4}$  section 16, USNM 883218.—Twin Springs, Snake Valley, T. 16 S, R. 18 W, SW  $\frac{1}{4}$  section 22, USNM 883208.—Cold Spring, Snake Valley, T. 16 S, R. 19 W, NW  $\frac{1}{4}$  section 2, USNM 883213. *Morgan County*: Spring, East Canyon, Weber River drainage, T. 1 N, R. 3 E, NW  $\frac{1}{4}$  section 14, USNM 883389.—Spring, East Canyon, Weber River drainage, T. 1 N, R. 3 E, SE  $\frac{1}{4}$  section 15, USNM

874074.—Dixie Spring, East Canyon Creek, Weber River drainage, T. 2 N, R. 3 E, NE  $\frac{1}{4}$  section 1, USNM 883634.—Lost Creek near Devils Slide, Weber River drainage, T. 4 N, R. 4 E, SE  $\frac{1}{4}$  section 19, USNM 883596.—Devils Slide, FMNH 179260, FMNH 179307. *Rich County*: Spring, lower Home Canyon, Bear River drainage, T. 8 N, R. 6 E, SW  $\frac{1}{4}$  section 24, USNM 883485. *Salt Lake County*: Spring, Riverton, Jordan River



drainage, T. 3 S, R. 1 W, NW ¼ section 34, USNM 883236, USNM 883284.—Spring, HWY 80, Parleys Canyon (just below Parleys Summit), Jordan River drainage, T. 1 S, R. 3 E, SE ¼ section 8, USNM 858287, USNM 883628.—Spring, Emigration Canyon (near mouth), Jordan River drainage, T. 1 S, R. 1 E, NE ¼ section 11, USNM 883613.—Spring, (upper) City Creek Canyon, Jordan River drainage, T. 1 N, R. 1 E, NW ¼ section 13, USNM 883606.—Spring, City Creek Canyon, Jordan River drainage, T. 1 N, R. 1 E, section 30, USNM 874073, USNM 874374, USNM 874375, USNM 883588.—Spring, City Creek Canyon, USNM 31271.—Lambs Canyon, Great Salt Lake Desert, FMNH 178387.—Mill Creek Canyon, Jordan River drainage, FMNH 178363.—Liberty Park, Salt Lake City, FMNH 178516.—south Salt Lake City, FMNH 179664.—33rd and 7th Street E, Salt Lake City, FMNH 178372.—Emigration Canyon, Great Salt Lake Desert, FMNH 178444.—City Creek, Salt Lake City, FMNH 178874, FMNH 178392.—City Creek, north bridge, FMNH 178362.—Red Butte Canyon, Great Salt Lake Desert, FMNH 178368, FMNH 178384.—Red Butte, Great Salt Lake Desert, FMNH 178369.—Tarpeys Spring, Salt Lake City, USNM 199398.—Salt Lake City, USNM 414181, USNM 424340.—Clintons Cave (sub-fossil), FMNH 178385, FMNH 223987, FMNH 224407. *Sevier County*: Springs, Live Oak Canyon, Sevier River drainage, T. 26 S, R. 3 W, NW ¼ section 4, USNM 883581.—Spring, 2.2 km south of Sigurd, Sevier River drainage, T. 23 S, R. 2 W, NW ¼ section 12, USNM 883428, USNM 883934. *Summit County*: Spring, southwest of Francis, Provo River drainage, T. 2 S, R. 6 E, SE ¼ section 32, USNM 883620.—Spring, Peoa, Weber River drainage, T. 1 S, R. 5 E, section 23, USNM 874384.—Spring, Peoa, Weber River drainage, T. 1 S, R. 5 E, section 23, USNM 874076.—Spring, Peoa, Weber River drainage, T. 1 S, R. 5 E, SE ¼ section 14, USNM 883629.—Beard Spring, Weber River drainage, T. 3 N, R. 4 E, SE ¼ section 19, USNM 883580. *Tooele County*: Springs, Dog Hollow Creek, Rush Valley, T. 9 S, R. 4 W, SE ¼ section 20, USNM 883196.—Spring, south end Atherly Reservoir, Rush Valley, T. 7 S, R. 5 W, SW ¼ section 28, USNM 883488.—Springs, south of Rush Lake, Rush Valley, T. 5 S, R. 5 W, NW ¼ section 2, USNM 883483.—Spring, below Little Pole Canyon, Skull Valley, T. 3 S, R. 7 W, SW ¼ section 30, USNM 883626.—Springs (southernmost), west of Salt Mountain, Skull Valley, T. 3 S, R. 8 W, SW ¼ section 16, USNM 883233.—Horseshoe Springs, Skull Valley, T. 2 S, R. 8 W, SE ¼ section 26, USNM 858285, USNM 873436, USNM 883204.—Muskrat Spring, Skull Valley, T. 2 S, R. 8 W, UMMZ 219484.—Big Spring, Skull Valley, T. 1 S, R. 7 W, SE ¼ section 8, USNM 858282, USNM 883199, USNM 883282.—Spring, northwest of Flux, Tooele Valley, T. 1 S, R. 7 W, NE ¼ section 25, USNM 883225, USNM 883398.—Spring, Lake Point, Tooele Valley, T. 1 S, R. 4

W, SE ¼ section 24, USNM 883621.—Near Lake Point, Tooele Valley, USNM 47864.—“Redden Springs,” ca. 9.6 km north of Callao, Great Salt Lake Desert, T. 9 S, R. 16 W, SW ¼ section 31, USNM 883203.—Blue Lake, Great Salt Lake Desert, T. 4 S, R. 19 W, SW ¼ section 6, USNM 883232.—Spring feeding Blue Lake, Great Salt Lake Desert, T. 4 S, R. 19 W, SE ¼ section 6, USNM 883224, USNM 883633.—Stream, 3.2 km west of Bonneville Service Station, near Timp (Timpie), FMNH 178400 (mixed with *Tryonia protea* [Gould, 1855]).—West side of Skull Valley (subfossil), FMNH 178423.—4.8 km south of Stockton, Rush Valley, FMNH 178380.—Spring before Josepha, Skull Valley, FMNH 178382 (mixed with *Tryonia protea*).—First spring south of Josepha, Skull Valley, FMNH 178381.—Southeast of Tooele, FMNH 224405. *Utah County*: Springs, Warm Springs Ditch, Goshen Valley (Utah Lake Basin), T. 10 S, R. 1 E, center section 8, USNM 883230.—Holladay Springs, Utah Lake Basin, T. 9 S, R. 1 E, NE ¼ section 25, USNM 883605.—Spring, Right Fork Hobbie Creek, Utah Lake Basin, T. 7 S, R. 4 E, SW ¼ section 24, USNM 883570.—“Clyde Spring,” Hobbie Creek, Utah Lake Basin, T. 8 S, R. 3 E, SE ¼ section 3, USNM 883935.—Spring, Diamond Fork, Utah Lake Basin, T. 8 S, R. 5 E, NE ¼ section 32, USNM 873331, USNM 883571.—Spring, South Fork Provo River, T. 5 S, R. 3 E, NE ¼ section 36, USNM 883609.—Spring (source), Spring Creek, below Mill Pond, Utah Lake Basin, T. 5 S, R. 1 E, SW ¼ section 15, USNM 883229, USNM 883285.—Big Spring, west of Fairfield, Cedar Valley, T. 6 S, R. 2 W, SE ¼ section 30, USNM 883235.—Spring, Cedar Fort, Cedar Valley, T. 6 S, R. 2 W, SW ¼ section 6, USNM 883281, USNM 883429.—Spanish Fork Canyon (sixth water canyon), FMNH 178370, FMNH 178376. *Wasatch County*: Spring, Willow Creek, Strawberry River drainage (Colorado River drainage basin), T. 6 S, R. 12 W, SE ¼ section 14, USNM 883617.—Spring Creek, Wallsburg, Provo River drainage, T. 5 S, R. 5 E, ¼ section 18, USNM 883618.—Cascade Springs, Provo River drainage, T. 4 S, R. 3 E, NE ¼ section 24, USNM 873339, USNM 883635.—Spring, along HWY 40–189, ca. 2.0 km north Heber City, Heber Valley, Provo River drainage, T. 3 S, R. 5 E, SW ¼ section 29, USNM 883623.—Hot Springs, northwest of Midway, Heber Valley, Provo River drainage, T. 3 S, R. 4 E, SW ¼ section 27, USNM 883794, USNM 883844.—Spring, east of Hailstone, Provo River drainage, T. 2 S, R. 5 E, NE ¼ section 33, USNM 874372.—Spring, east of Hailstone, Provo River drainage, T. 2 S, R. 5 E, SE ¼ section 33, USNM 873340.—Drain Tunnel Creek, Provo River drainage, T. 2 S, R. 5 E, NE ¼ section 19, USNM 858284.—Drain Tunnel Creek, Provo River drainage, T. 2 S, R. 5 E, SE ¼ section 19, USNM 873334.—Ross Creek, Provo River drainage, T. 2 S, R. 5 E, NE ¼ section 18, USNM 883631.—Provo River, below Charleston, FMNH 179177. *Washington County*: Springs, west side Left Fork

of North Creek, Virgin River drainage, T. 40 S, R. 11 W, NE ¼ section 28, USNM 847248.—Leeds, Virgin River drainage, FMNH 178356.—Springs, Left Fork Santa Clara River, Pine Valley, T. 39 S, R. 14 W, SW ¼ section 20, USNM 847029, USNM 883258.—Spring, Pinto Creek, Escalante Desert, T. 38 S, R. 15 W, NE ¼ section 12, USNM 874735.—Pinto Spring, Escalante Desert, T. 38 S, R. 14 W, center section 6, USNM 883211.—Spring, southwest of Pinto, Pinto Creek, Escalante Desert, T. 37 S, R. 15 W, SE ¼ section 33, USNM 883228.—Springs, Calf Springs Creek, Escalante Desert, T. 38 S, R. 17 W, NE ¼ section 4, USNM 883201. *Weber County*: Spring, mouth of Ogden County, Ogden River drainage, T. 6 N, R. 1 W, SW ¼ section 23, USNM 883598.—Springs, North Fork Ogden River, T. 7 N, R. 1 E, NE ¼ section 18, USNM 883604.

*Pyrgulopsis pilsbryana* (Baily & Baily, 1952)

*Amnicola pilsbryi* Baily & Baily, 1951:50, pl. 4, fig. 3 [not *Amnicola pilsbryi* Walker, 1906].

*Amnicola pilsbryana* Baily & Baily, 1952:144 [new name for *Amnicola pilsbryi* Baily & Baily, 1951].

*Fontelicella pilsbryana* (Baily & Baily, 1952), Taylor, 1975: 152 [literature compilation].

*Fontelicella pilsbryi* (Baily and Baily, 1951), Taylor, 1975: 153 [literature compilation].

*Pyrgulopsis pilsbryana* (Baily & Baily, 1952), Hershler and Thompson, 1987:28–30 [transfer to *Pyrgulopsis*].—Hershler, 1994:60 [figures].

**Diagnosis:** Medium-sized to large, with ovate- to narrow-conic shell. Penis large, filament and lobe medium length. Penial ornament a medium-sized terminal gland, very small-large penial gland, and minute Dg3.

**Type locality:** Lifton, Ideal Beach, Bear Lake, Idaho.

**Remarks:** The range of this species (previously restricted to the type locality area in Bear Lake basin) encompasses the Bear Lake basin and Bear River basin, both above and below (above Cache Valley) the Bear Lake outlet (Figure 55). The distribution of this species closely abuts that of *P. kolobensis*, a similar species which differs in having a ventral gland on the penis. Populations of *P. pilsbryana* vary principally in terms of shell shape and length of penial gland.

**Material examined:** IDAHO. *Bear Lake County*: Spring, St. Charles Canyon, Bear Lake Basin, T. 15 S, R. 43 E, SE ¼ section 17, USNM 858281, USNM 883444.—Spring, northeast side Merkley Lake, Bear Lake drainage, T. 14 S, R. 44 E, NE ¼ section 26, USNM 883585.—Spring, Stauffer Creek, Bear River drainage, T. 11 S, R. 43 E, NE ¼ section 27, USNM 883587. *Caribou County*: Ledger Creek, Soda Springs, Bear River drainage, T. 9 S, R. 42 E, SE ¼ section 5, USNM 883537, USNM 883895.—Pond outflow, Kelly Park, Soda Springs, Bear River drainage, T. 9 S, R. 42 E, NW ¼ section 5, USNM 883534, USNM 883535, USNM 883889.—Formation

Spring, Bear River drainage, T. 8 S, R. 42 E, section 28, USNM 874153.—Formation Spring (outflow), Bear River drainage, T. 8 S, R. 42 E, SE ¼ section 28, USNM 883567.—Kackley Spring, Gem Valley, Bear River drainage, T. 10 S, R. 40 E, SW ¼ section 21, USNM 883538, USNM 883891.—Spring (source), Whiskey Creek, Gentle Valley, Bear River drainage, T. 11 S, R. 41 E, SE ¼ section 7, USNM 883441. *Franklin County*: Spring Creek, HWY 34 crossing, Mound Valley, Bear River drainage, T. 12 S, R. 41 E, NW ¼ section 18, USNM 883423. UTAH. *Rich County*: Jacobsen Springs, Big Creek, Bear River drainage, T. 10 N, R. 6 E, SW ¼ section 1, USNM 883578.—Big Spring, Bear Lake Basin, T. 12 N, R. 5 E, NE ¼ section 4, USNM 883586.—Spring, ca. 0.8 km north of Lakota, Bear Lake Basin, T. 15 N, R. 5 E, SE ¼ section 32, USNM 883574. WYOMING. *Lincoln County*: Springs, Bear River drainage, T. 22 N, R. 120 W, section 26, USNM 883896.

*Pyrgulopsis hamlinensis* Hershler, sp. nov.

Hamlin Valley pyrg  
(Figures 9I, 22K, 43A–C)

**Etymology:** Referring to endemism of this snail in Hamlin Valley, Utah.

**Diagnosis:** Small, with narrow-conic shell. Penis small to medium-sized, filament medium length, lobe short to medium length. Penial ornament a medium-sized terminal gland.

**Description:** Shell (Figures 9I, 22K) narrow-conic, width/height, 59–69%; height, 1.6–2.0 mm; width, 1.0–1.3 mm; whorls, 4.25–5.0. Protoconch 1.25 whorls, diameter 0.34 mm, smooth except for small area of very weak wrinkling at apex. Teleoconch whorls low-medium convexity, narrowly shouldered, often having pronounced angulation at base; body whorl often broadly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thin, without columellar shelf. Outer lip thin, orthocline or weakly prosocline, without situation. Umbilicus rimate to shallowly perforate. Periostracum light tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around.

Radula 560 × 95 μm, with 62 rows of teeth. Central tooth 23 μm wide, with highly indented dorsal edge; lateral cusps, 5–7; central cusp narrow, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets deep. Lateral tooth formula 3(4)-1-4(5); neck weakly flexed; outer wing 225% of cutting edge length. Inner marginal teeth with 24–28 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 25–30 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or having very light grey pigment proximally. Snout medium grey. Foot light

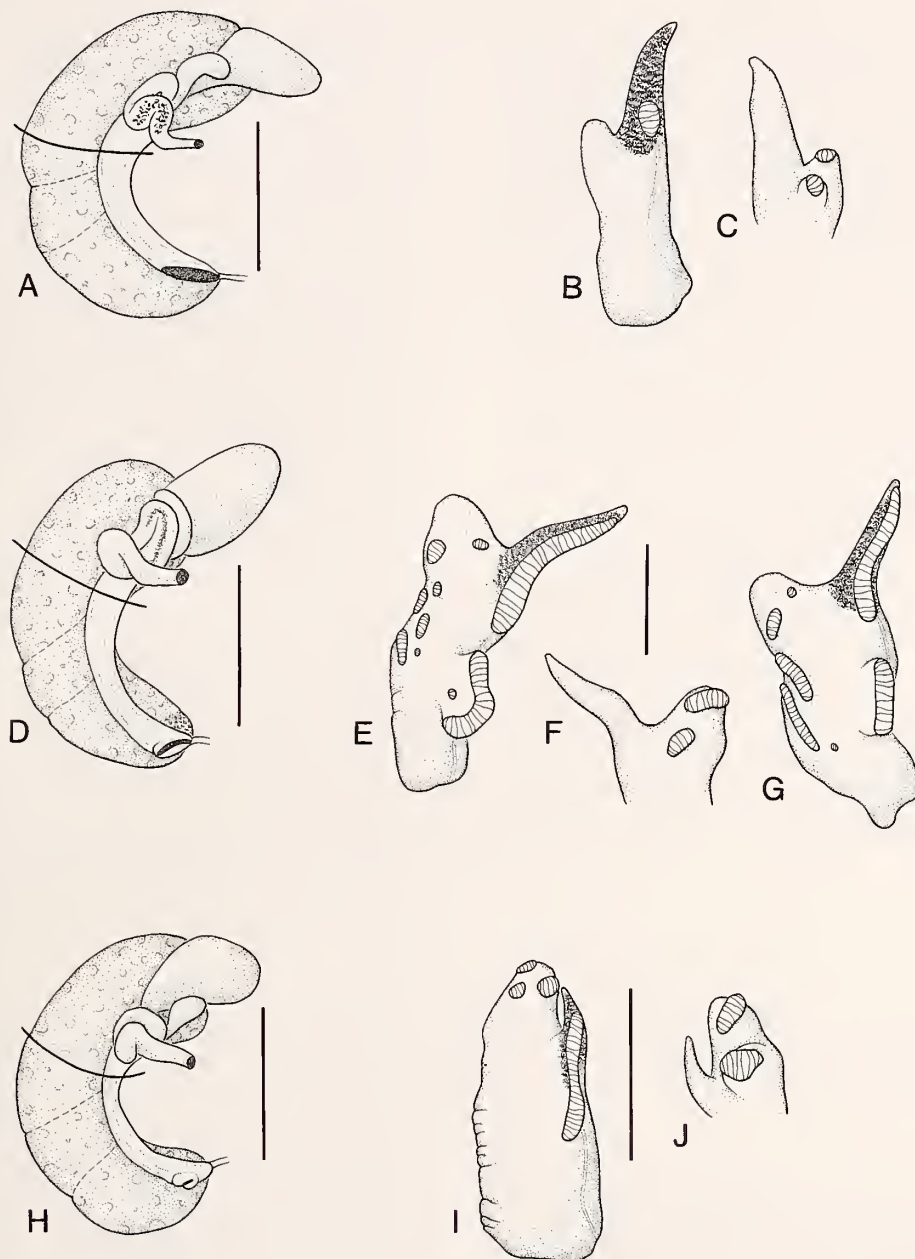


Figure 47

Genitalia of *Pyrgulopsis* species (A, *P. fusca*, USNM 860728; B, *P. fusca*, USNM 883484; D–G, *P. chamberlini*, USNM 860729; H–J, *P. inopinata*, USNM 860730). Bars = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Two examples of the dorsal penis (E, G) are shown for *P. chamberlini*.

to medium grey. Opercular lobe dark along inner edge, sometimes along outer edge as well. Neck unpigmented except for scattered grey granules. Pallial roof, visceral coil near uniform black (pigment slightly lighter on genital ducts). Penial filament darkly pigmented internally for most of length.

Ctenidial filaments, 15, weakly pleated; ctenidium connected to pericardium by short efferent vein. Osphradium small, narrow, positioned slightly posterior to middle of ctenidium. Renal gland longitudinal; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive

gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 43A. Albumen gland having medium (up to 33%) pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, mounted on weak papilla, having short anterior extension. Coiled oviduct a posterior-oblique loop sometimes preceded by weak to well-developed posterior twist. Bursa copulatrix medium length and width, ovate, longitudinal, slightly less than 33% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, often poorly distinguished from bursa; short (up to 50% of bursa length), medium width. Seminal receptacle small, sometimes minute, pouchlike or sub-globular, overlapping anteriormost section of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland small, sub-globular, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens straight or having weak undulation. Penis (Figure 43B, C) small to medium-sized; base rectangular, weakly folded; filament 66% length of base, medium width, tapering to point, longitudinal or slightly oblique; lobe slightly shorter to as long as filament, clublike, longitudinal or slightly oblique. Terminal gland medium-sized, ovate or circular, rarely bifurcate, variably oriented, ventral. Penial duct straight, near outer edge.

**Type locality:** Springs, 0.5 km east of White Rock Cabin Springs, Hamlin Valley, Beaver County, Utah, T. 30 S, R. 20 W, SE  $\frac{1}{4}$  section 2 (Figure 55). Holotype, USNM 883215 (Figure 22K), collected by R. Hershler and P. Hovingh, 9 May 1993; paratypes, USNM 860695. The type locality is a small, high elevation rheocene slightly impacted by cattle (Figure 5D).

**Remarks:** This species is contrasted with *P. montana* above.

**Material examined:** UTAH. *Beaver County*: Springs, 0.5 km east of White Rock Cabin Springs (Figure 5D), USNM 860695, USNM 883215.

*Pyrgulopsis peculiaris* Hershler, sp. nov.

Bifid duct pyrg

(Figures 9J, 23A–G, 43D–I)

**Etymology:** From *peculiaris* (Latin), singular; referring to the unique configuration of the female bursal duct in this species.

**Diagnosis:** Medium-sized, with ovate- to narrow-conic shell. Penis large; filament and lobe medium length. Penial ornament a medium-large, fragmented terminal gland;

small penial gland, large Dg1, large Dg2, large Dg3, additional four to seven dorsal glands, and two large ventral glands.

**Description:** Shell (Figures 9J, 23A–G) ovate to narrow conic, width/height, 62–89%; height, 1.7–3.0 mm; width, 1.3–2.1 mm; whorls, 3.5–5.0. Protoconch 1.25–1.5 whorls, diameter 0.34 mm, initial 0.5–1.0 whorl finely wrinkled, later portion smooth. Teleoconch whorls highly convex, shoulders weak to well developed; body whorl often slightly disjunct behind the aperture and having sub-sutural ramp bordered below by pronounced angulation. Aperture ovate, usually disjunct. Inner lip slightly thickened; columellar shelf very narrow to broad. Outer lip thin or slightly thickened, slightly prosocline, without sinuation. Umbilicus narrowly perforate. Periostracum light tan.

Operculum ovate, reddish; nucleus eccentric; dorsal surface weakly frilled; outer margin sometimes having weak rim. Attachment scar thick, sometimes broadly so, all around.

Radula  $720 \times 100 \mu\text{m}$ , with 57 rows of teeth. Central tooth  $32 \mu\text{m}$  wide, with slightly indented dorsal edge; lateral cusps, 4; central cusp medium width, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2-1-3; neck weakly flexed; outer wing 130% of cutting edge length. Inner marginal teeth with 18–20 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 27–31 cusps; cutting edge occupying 27% of length of tooth. Stomach larger than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles, snout, foot light to medium brown. Opercular lobe dark along inner edge, often all around. Neck unpigmented except for scattered dark granules to light brown. Pallial roof, visceral coil uniform dark brown to black. Penial filament darkly pigmented along most of length; adjacent portion of base similarly pigmented.

Ctenidial filaments, 16, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned slightly posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening grey-white, slightly raised. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 43D. Albumen gland having very short pallial component. Capsule gland longer, but narrower than albumen gland, broadly ovate in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique to almost circular loop; proximal arm sometimes kinked, usually darkly pigmented. Oviduct and bursal ducts joining a little behind pallial wall. Bursa

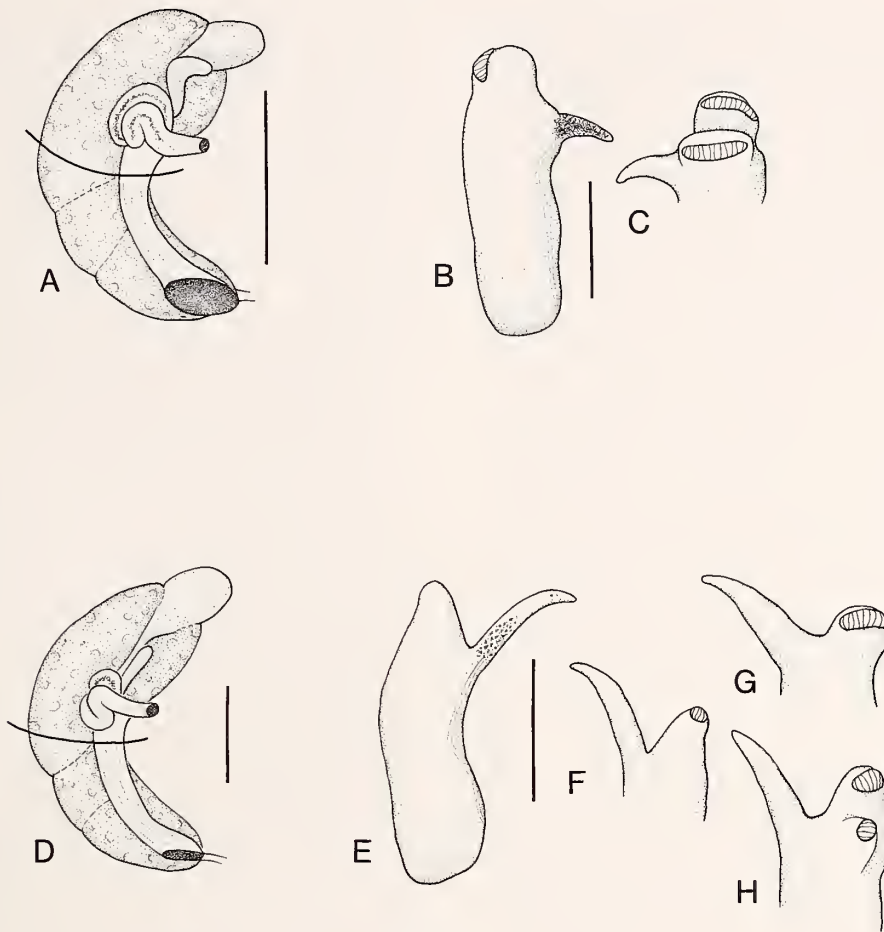


Figure 48

Genitalia of *Pyrgulopsis* species (A–C, *P. nonaria*, USNM 860731; D–F, *P. transversa*, USNM 860732; G, H, *P. transversa*, USNM 883422). A–C. Bars = 0.5 mm. D. Bar = 0.25 mm. E–H. Bar = 0.5 mm. Drawings show (from left to right) female glandular oviduct and associated structures, dorsal aspect of penis, ventral aspect of distal penis. Three examples of the ventral penis (F–H) are illustrated for *P. transversa*.

copulatrix medium length, but as wide as albumen gland, pyriform, longitudinal, with almost entire length posterior to gland. Bursal duct bifid (Figure 43E), consisting of duct originating from anterior edge at or near mid-line, medium length, narrow; and much narrower duct (of same length) originating from anterior edge near ventral margin; ducts share common opening to oviduct. Seminal receptacle a small, narrow pouch folded into an inverted U-shape, overlapping middle of bursa copulatrix.

Testis 1.0–1.25 whorls, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland large, elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop; duct broad. Penis (Figure 43F–I) large; base rectangular, expanded distally, with pronounced swelling along inner edge, inner edge folded; filament medium length, narrow,

tapering to point, usually oblique; lobe as long as filament, triangular, longitudinal. Terminal gland consisting of three short, ovate-circular units along edge of lobe (mostly ventral) unit along outer edge often fused with distal unit, occasionally all three units fused. Penial gland small, narrow, positioned near base of filament. Dg1 large (rarely reduced), positioned medially, usually transverse, sometimes fused with either Dg3 or outermost of additional longitudinal glands. Dg2 large, distal, borne on expanded edge of lobe. Dg3 large, extending to near base of filament (abutting or fusing with Dg1), sometimes curving across lobe, portion on lobe raised. Dorsal penis also bearing four to seven additional units (typically elongate, longitudinal, sometimes small, circular or dotlike) positioned between penial gland, Dg1 and Dg2; innermost units often fused distally. Ventral glands, two, large, distal gland narrow (sometimes accompanied distally by

raised, dotlike unit), borne on large swelling, traversing most of width of penis near base of filament; proximal gland shorter, broader, borne on prominent swelling, transverse, positioned near base of penis. Penial duct straight, near outer edge.

**Type locality:** Spring, Maple Grove, Round Valley, Millard County, Utah, T. 21 S, R. 2 1/2 W, NW ¼ section 1. Holotype, USNM 883933 (Figure 23A), collected by R. Hershler and P. Hovingh, 11 May 1995; paratypes, USNM 860703. The type locality is a small, montane rheocene slightly disturbed by recreational activities.

**Remarks:** The penis of this snail somewhat resembles those of the group of species having a full complement of glands, but differs in that the penial gland is very small. Additionally, the terminal gland is weaker than in many members of this group, and a pronounced distal swelling is present along the inner edge of the penis base, a feature absent in the above species but similar to that of *P. limaria*, from northwest Lahontan Basin. This species is also unique among *Pyrgulopsis* in having a bifid bursal duct, a condition apparently paralleling that seen in *Cincinnatia integra* (see Hershler & Thompson, 1996). The distribution of this species is shown in Figure 55.

**Material examined:** NEVADA. *White Pine County:* Springs, Big Springs Creek, Snake Valley, T. 10 N, R. 70 E, SW ¼ section 22, USNM 874683.—Turnley Spring, Spring Valley, T. 16 N, R. 68 E, SW ¼ section 16, USNM 874319, USNM 874666. UTAH. *Millard County:* Spring, Maple Grove, USNM 860703, USNM 883602, USNM 883933.—Church Spring, Pahvant Valley, T Spring, T. 19 S, R. 4 W, NE ¼ section 14, USNM 892053.—South Fork Chalk Creek, Pahvant Valley, T. 22 S, R. 3 W, NW ¼ section 6, USNM 883603.—Big Spring, Oak Creek, Sevier River drainage, T. 17 S, R. 4 W, NW ¼ section 12, USNM 883622.—Spring, above Swasey Spring, Whirlwind Valley, T. 16 S, R. 13 W, SW ¼ section 23, USNM 883222.—Antelope Spring, House Range, Sevier Desert drainage, T. 16 S, R. 13 W, NE ¼ section 34, USNM 883227.

*Pyrgulopsis anguina* Hershler, sp. nov.

Longitudinal gland pyrg

(Figures 9K, 23H–J, 44A–E)

**Etymology:** From *anguinus* (Latin), of snakes; referring to endemism of this species in Snake Valley, Nevada-Utah.

**Diagnosis:** Medium-sized, with sub-globose to ovate-conic shell. Penis large; filament and lobe short. Penial ornament a medium-sized terminal gland, large penial gland, medium-large Dg1, large Dg2, medium-large Dg3, additional dorsal gland, and large ventral gland.

**Description:** Shell (Figures 9K, 23H–J) sub-globose to

ovate-conic, apex often eroded; width/height, 70–95%; height, 2.0–3.5 mm; width, 1.7–2.4 mm; whorls, 3.0–5.0. Protoconch 1.25 whorls, diameter 0.30 mm, weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium to highly convex, shoulders narrow or absent, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture pyriform, adnate or disjunct. Inner lip slightly thickened in larger specimens, often forming narrow columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus shallowly perforate. Periostracum tan-green.

Operculum ovate, amber, nuclear region slightly reddish; nucleus eccentric; dorsal surface frilled. Attachment scar often thick all around.

Radula 820 × 120 μm, with 62 rows of teeth. Central tooth 26 μm wide, with medium-highly indented dorsal edge; lateral cusps, 5–7; central cusp medium width, rounded; basal cusps large. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-4(5); neck medium flexed; outer wing 195% of cutting edge length. Inner marginal teeth with 27–34 cusps (basal enlarged, separated); cutting edge occupying 43% of length of tooth. Outer marginal teeth with 32–40 cusps; cutting edge occupying 26% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to medium brown. Snout, foot light to medium brown. Opercular lobe dark along inner edge, sometimes also along sides. Neck unpigmented except for scattered granules to medium brown. Pallial roof, visceral coil uniformly dark brown or black. Penial filament darkly pigmented along almost entire length; black granules sometimes scattered on remainder of penis.

Ctenidial filaments, 18, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned posterior to middle of ctenidium. Renal gland slightly oblique; kidney opening thick, white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 44A. Albumen gland having large (ca. 40%) pallial component. Capsule gland shorter, narrower than albumen gland, sub-globular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes mounted on weak papilla, having short anterior extension. Coiled oviduct of two overlapping posterior-oblique loops; posterior loop often overlapping bursa copulatrix. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix as long and wide as albumen gland, ovate-pyriform, longitudinal, with most or all of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line and close to oviduct;

very short (20%), narrow. Seminal receptacle very small, pouchlike, overlapping anterior half of bursa.

Testis 1.25–1.5 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland very large, elongate bean-shaped, pallial portion large (almost 50%), ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop; duct broad. Penis (Figure 44B–E) large; base rectangular, sometimes slightly expanded distally, weakly folded; filament short, medium width, tapering to point, longitudinal or slightly oblique; lobe as long as filament, triangular, longitudinal. Terminal gland medium-sized, narrow, longitudinal, largely or entirely ventral. Penial gland filling most of length of filament and slightly overlapping base, slightly narrower than filament. Dg1 medium-large, narrow, slightly or prominently raised, sometimes slightly curved, longitudinal or slightly oblique, positioned near mid-length at or near outer edge. Dg2 large, sometimes bifurcate, slightly raised or crestlike, positioned along inner edge. Dg3 medium-large, narrow, positioned near outer edge of lobe. Dorsal penis also bearing long gland (rarely bifurcate) near inner edge distally (extending distal to Dg2 and slightly overlapping lobe), often fused with Dg3 to form U-shaped loop. Small, circular glands sometimes found alongside Dg1 and Dg2, just proximal to edge of Dg3. Ventral gland large, usually narrow (rarely small, circular), borne on prominent swelling, usually straight and transverse, but sometimes curved; positioned near base of lobe. Penial duct straight, near outer edge.

**Type locality:** Big Springs, Snake Valley, White Pine County, Nevada, T. 10 N, R. 70 E, NE  $\frac{1}{4}$  section 33. Holotype, USNM 874678 (Figure 23H), collected by R. Hershler and P. Hovingh, 23 June 1992; paratypes, USNM 860725. The type locality is a shallow, 4 m wide rheocene moderately disturbed by livestock.

**Remarks:** Among the group of species having a full complement of penial ornament, *P. anguina* most closely resembles *P. chamberlini* (described below), from Sevier River drainage, but differs in its broader shell, larger penial lobe, longitudinal orientation of terminal gland, and stronger Dg3 and ventral gland. The distribution of *P. anguina* is shown in Figure 55.

**Material examined:** NEVADA. *White Pine County:* Big Springs, Snake Valley, USNM 860725, USNM 874678. UTAH. *Millard County:* Clay Spring, Snake Valley, T. 22 S, R. 19 W, NW  $\frac{1}{4}$  section 33, USNM 883205.

*Pyrgulopsis saxatilis* Hershler, sp. nov.

Sub-globose Snake pyrg

(Figures 9L, 11H, 16A–C, 23K, L, 44F–H)

**Etymology:** From *saxatilis* (Latin), found among rocks; referring to the habitat of species.

**Diagnosis:** Small, with sub-globose shell. Penis large, filament and lobe short. Penial ornament a small terminal gland, small Dg1, and large ventral gland.

**Description:** Shell (Figures 9L, 23K, L) sub-globose, apex usually eroded in adult specimens; width/height, 90–106%; height, 1.0–1.4 mm; width, 1.0–1.4 mm; whorls, 3.5–4.0. Protoconch (Figure 11H) 1.25 whorls, diameter 0.28 mm; initial 0.75 whorl finely wrinkled. Teleoconch whorls medium convexity; shoulders well developed, final 0.25 whorl sometimes having pronounced sub-sutural angulation. Aperture ovate-pyriform, adnate. Inner lip slightly thickened, columellar shelf medium width. Outer lip thin, prosocline, weakly sinuate. Umbilicus narrowly rimate to shallowly perforate. Periostracum eroded or absent.

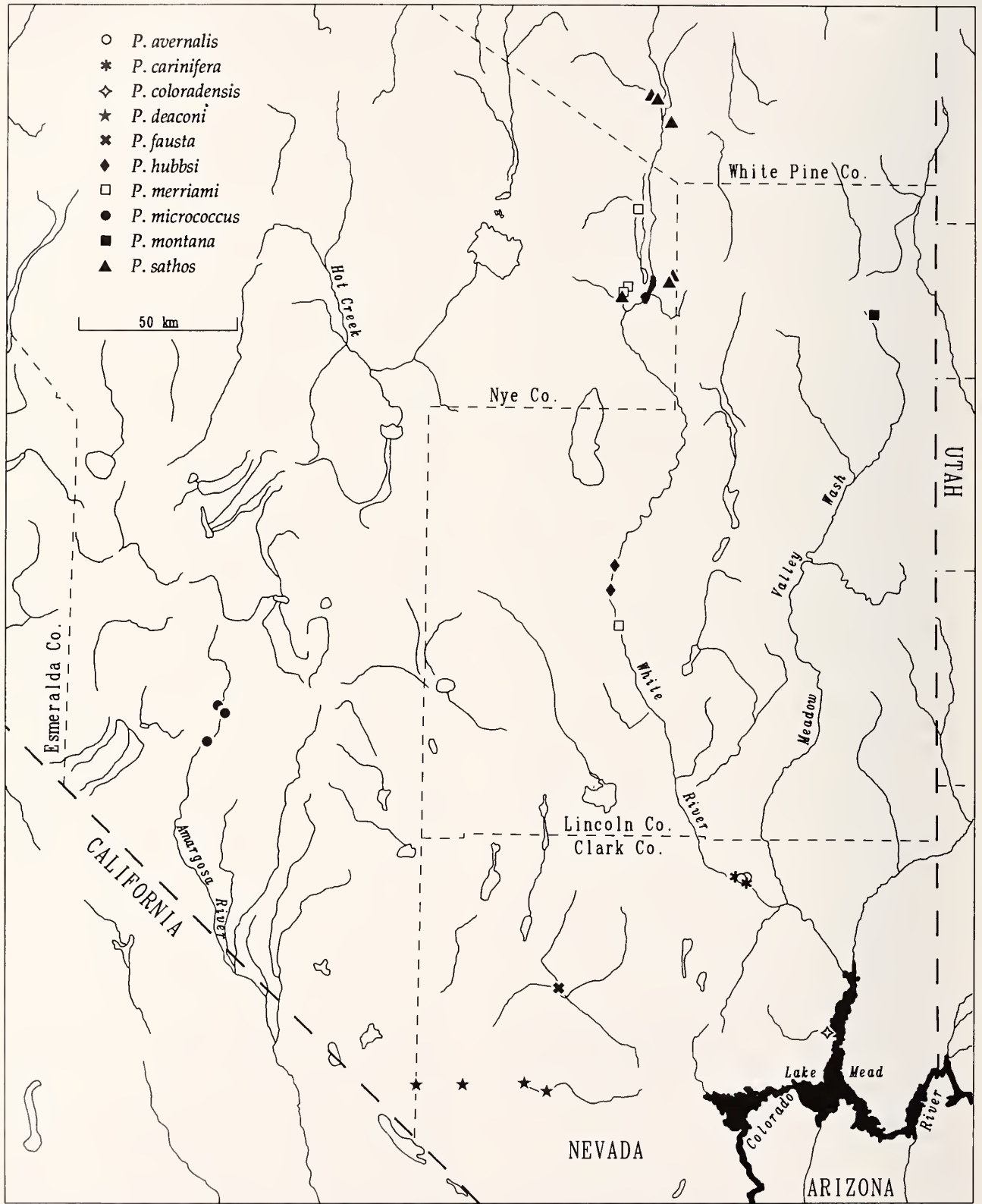
Operculum ovate, amber, slightly darker in nuclear region; dorsal surface smooth or weakly frilled; outer margin sometimes having very faint rim. Attachment scar thick along inner edge and between inner edge and nucleus.

Radula (Figure 16A–C)  $480 \times 65 \mu\text{m}$ , with 60 rows of teeth. Central tooth  $15 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 5–7; central cusp long, daggerlike; basal cusps medium-sized. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-4(5); neck weakly flexed; outer wing 200% of cutting edge length. Inner marginal teeth with 22–25 cusps; cutting edge occupying 36% of length of tooth. Outer marginal teeth with 24–27 cusps; cutting edge occupying 29% of length of tooth. Stomach longer than style sac; stomach chambers poorly distinguished externally, but anterior chamber slightly larger; stomach caecum very small.

Cephalic tentacles, foot light to medium brown. Snout medium to dark brown. Opercular lobe unpigmented or diffuse light brown. Neck light to medium grey-brown. Pallial roof, visceral coil uniformly dark brown or black. Penial filament darkly pigmented along most of length; base also containing scattered black granules.

Ctenidial filaments, 12, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow ovate, positioned slightly posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 44F. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal slit mounted on weak papilla, anterior extension short. Coiled oviduct a small circular loop, usually preceded by well-developed posterior twist. Oviduct and bursal duct joining a little behind





pallial wall. Bursa copulatrix short, narrow, globular-pyriform, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at mid-line, long, narrow to medium width. Seminal receptacle small to medium-sized, pouchlike, overlapping proximal to medial portion of bursal duct, often overlapped by albumen gland.

Testis 1.0 whorl, filling 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens with well-developed loop. Penis (Figure 44G, H) large; base elongate-rectangular, smooth or weakly folded along inner edge; filament short, narrow, tapering to point, longitudinal or slightly oblique; lobe as long as filament, clublike, but narrowing distally, longitudinal. Terminal gland small, circular to ovate (usually transverse), ventral. Dg1 small, ovate, longitudinal or slightly oblique, positioned just proximal to base of filament. Ventral gland large, narrow, slightly raised, angling across penis to base of lobe at inner edge. Dorsal and ventral penis also frequently having one to six minute, variably positioned, glandular dots. Penial duct slightly undulating near outer edge distally.

**Type locality:** Warm Springs, Snake Valley, Millard County, Utah, T. 16 S, R. 19 W, SW  $\frac{1}{4}$  section 31 (Figure 55). Holotype, USNM 883237 (Figure 23K), collected by R. Hershler and P. Hovingh, 10 May 1993; paratypes, USNM 860726. The type locality is a series of large, thermal (26.9°C) rheocrenes issuing from the side of a hill.

**Remarks:** This thermal endemic is contrasted above with *P. lata*, from White River Valley. *Pyrgulopsis saxatilis* also resembles widespread *P. kolobensis*, but differs in its minute, globose shell, narrower central cusps on the central radular teeth, more elongate outer wing on the lateral radular teeth, smaller penial lobe and filament, and weakly developed terminal gland.

**Material examined:** UTAH. Millard County: Warm Springs, USNM 860726, USNM 883237.

*Pyrgulopsis variegata* Hershler, sp. nov.

Northwest Bonneville pyrg

(Figures 10A, 24A–D, 45A–F)

**Etymology:** From *variegatus* (Latin), of different sorts; referring to the substantial variation in penial glands among populations assigned to this species.

**Diagnosis:** Medium-sized, with ovate- to narrow-conic shell. Penis small to large, filament and lobe medium length. Penial ornament a small terminal gland, very small penial gland (often absent), and small ventral gland (often absent).

**Description:** Shell (Figures 10A, 24A–D) ovate- to narrow-conic, width/height, 63–75%; height, 2.2–3.0 mm; width, 1.5–2.4 mm; whorls, 4.25–5.0. Protoconch 1.4–1.5 whorls, diameter 0.33 mm; smooth except for weak spiral striae along outer edge of whorl. Teleoconch whorls medium to highly convex, shoulders weak or absent; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip slightly thickened in largest specimens, without columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum light or reddish-brown.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; outer margin having weak rim. Attachment scar thick all around.

Radula 665 × 105  $\mu$ m, with 62 rows of teeth. Central tooth 26  $\mu$ m wide, with medium indented dorsal edge; lateral cusps, 5–7, central cusp medium width, rounded; basal cusps medium-sized. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-3(4, 5); neck weakly flexed; outer wing 185% of cutting edge length. Inner marginal teeth with 25–31 cusps (basal cusp enlarged); cutting edge occupying 35% of length of tooth. Outer marginal teeth with 31–36 cusps; cutting edge occupying 25% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small or very small.

Cephalic tentacles unpigmented or having proximal light grey patch. Snout, foot light to medium grey. Opercular lobe black along inner edge. Neck unpigmented except for scattered black granules to medium grey. Pallial roof, visceral coil medium grey to black, pigment non-uniform. Penial filament darkly pigmented; pigment granules scattered on base.

Ctenidium medium width; filaments, 17, without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum straight, broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 45A.

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Figure 49

Map showing distributions of *Pyrgulopsis* species of southern Nevada. Previously known records for *P. micrococcus*, *P. avernalis*, *P. carinifera*, and *P. merriami* are not shown. In cases where congeners are sympatric, symbols are slightly offset.

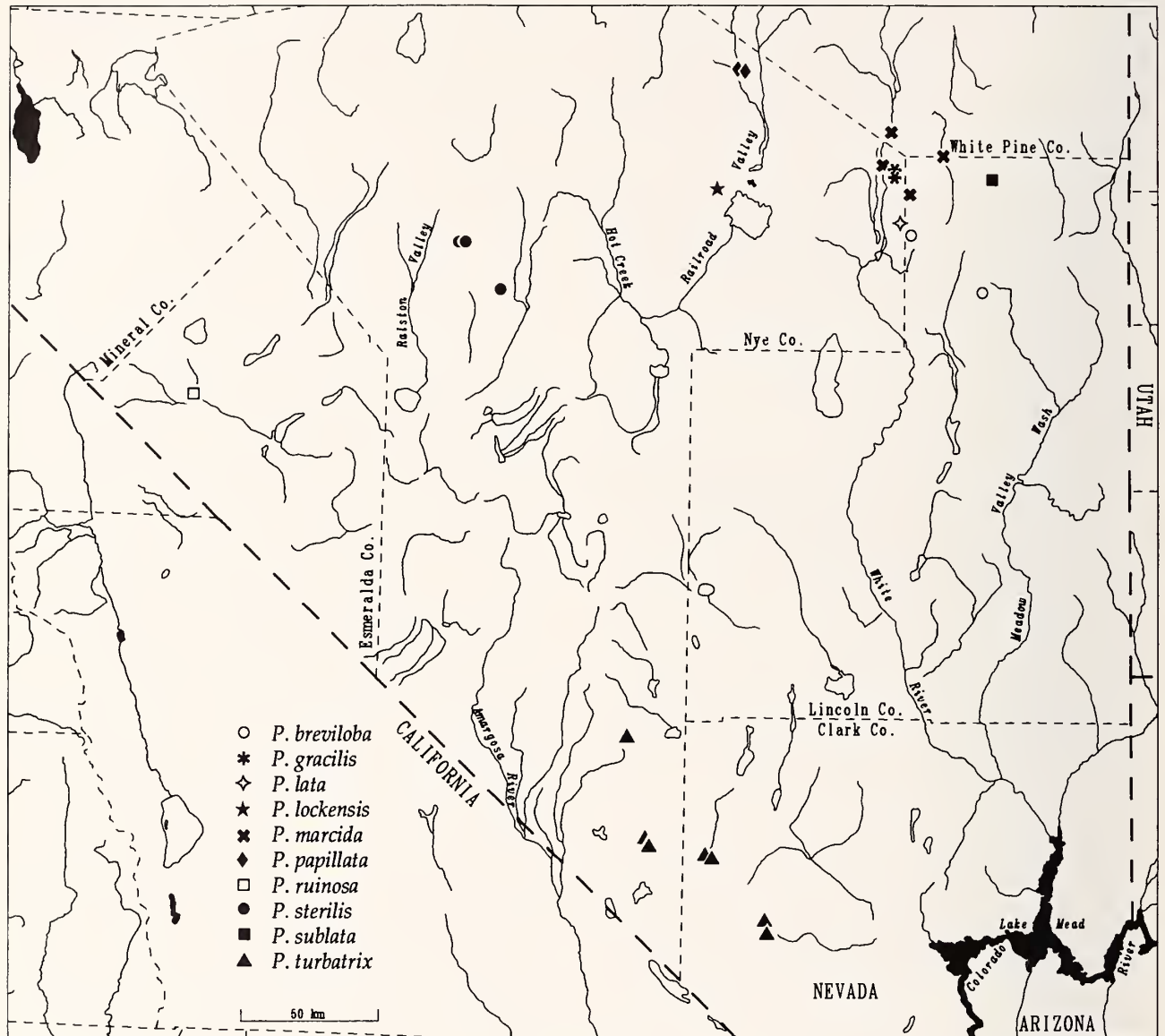


Figure 50

Map showing distributions of *Pyrgulopsis* species of the Colorado River drainage basin and isolated basins of Nevada. In cases where congeners are sympatric, symbols are slightly offset.

Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, circular in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal pore often mounted on weak papilla; anterior extension short. Coiled oviduct a posterior-oblique loop often preceded by weak posterior-oblique twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, medium width, pyriform, often having silvery sheen, longitudinal, with 50% or more of length usually posterior to gland, dorsal

edge sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at mid-line, slightly shorter to slightly longer than bursa, medium width. Seminal receptacle small, pouchlike, overlapping or slightly ventral to proximal portion of bursal duct.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and portion of anterior stomach chamber. Prostate gland small, subglobular, entirely visceral or with very short pallial portion, narrowly ovate in section. Proximal pallial vas deferens looped. Penis (Figure 45B-F) small to large; base

rectangular, sometimes elongate, folds along inner edge weak to well developed; filament 50% to almost as long as base, medium width, tapering to point, longitudinal or slightly oblique; lobe shorter than filament, slightly narrower than base, knoblike, longitudinal. Terminal gland small, rarely dotlike, narrow, circular-ovate, usually transverse (rarely longitudinal), entirely ventral or partly overlapping dorsal surface. Penial gland very small (often absent), narrow, positioned near base of filament. Ventral gland small (often absent), ovate-narrow, often slightly raised, longitudinal, distal. Penial duct straight, near outer edge.

**Type locality:** Spring, ca. 2.5 km south of South Patterson Spring, Pilot Valley, Box Elder County, Utah, T. 4 N, R. 19 W, SW  $\frac{1}{4}$  section 1. Holotype, USNM 883627 (Figure 24A), collected by R. Hershler and P. Hovingh, 9 July 1993; paratypes, USNM 860723. The type locality is a small, minimally disturbed basin floor rheocene.

**Remarks:** This species differs from similar *P. kolobensis* in having a smaller penial lobe and reduced (sometimes absent) glands on the penis. Populations of this species from the south and west have relatively well developed penial and terminal glands, and a weak or absent ventral glands; while those to the north and east (e.g., Grouse Creek, Park Valleys) have weak terminal gland, often lack a penial gland, and have stronger ventral glands. However, intergradation between these two conditions is evident in some populations, in which the penis has a well-developed penial gland, but weak terminal and ventral glands. The distribution of this species is shown in Figure 55.

**Material examined:** NEVADA. *Elko County:* Parson Springs, Pilot Creek Valley, T. 38 N, R. 70 E, NE  $\frac{1}{4}$  section 28, USNM 874713.—McCuition Springs, Pilot Creek Valley, T. 37 N, R. 70 E, NE  $\frac{1}{4}$  section 30, USNM 874723, USNM 883888.—Spring, lower Jay Creek, Goose Creek drainage, T. 47N, R. 69E, SW  $\frac{1}{4}$  section 23, USNM 874721. UTAH. *Box Elder County:* Spring, ca. 2.5 km south of South Patterson Spring, USNM 860723, USNM 883627.—Spring, Halls Meadow, T. 3 N, R. 19 W, section 22, USNM 873431.—Spring, Cotton Creek, Grouse Creek Valley, T. 13 N, R. 17 W, SE  $\frac{1}{4}$  section 29, USNM 883636.—Spring, Cotton Creek, Grouse Creek Valley, T. 13 N, R. 17 W, section 32, UCM 34042.—Spring brook, tributary to Etna Reservoir, Grouse Creek Valley (Figure 5E), T. 11 N, R. 18 W, NW  $\frac{1}{4}$  section 6, USNM 883614.—North Bedke Spring, Grouse Creek Valley, T. 11 N, R. 17 W, NW  $\frac{1}{4}$  section 32, USNM 883624.—South Bedke Spring, Grouse Creek Valley, T. 11 N, R. 17 W, SE  $\frac{1}{4}$  section 31, USNM 883583.—Spring, Left Hand Fork, Dove Creek, Park Valley (Figure 3C), T. 13 N, R. 16 W, NE  $\frac{1}{4}$  section 26, USNM 883599. *Tooele County:* Spring, ca. 4.8 km south of Donner Spring, Pilot

Valley, T. 3 N, R. 19 W, center section 14, USNM 883608.

*Pyrgulopsis hovinghi* Hershler, sp. nov.

Upper Thousand Spring pyrg

(Figures 10B, 111, 16D–F, 24E, 45G–I)

**Etymology:** Named after Peter Hovingh, in recognition of his extensive support and encouragement throughout this study.

**Diagnosis:** Medium-sized, with sub-globose to ovate-conic shell. Penis small to medium-sized; filament and lobe medium length. Penial ornament a large penial gland.

**Description:** Shell (Figures 10B, 24E) sub-globose to ovate-conic, apex and early teleoconch often eroded; width/height, 67–80%; height, 2.2–2.8 mm; width, 1.7–2.0 mm; whorls, 4.0–4.75. Protoconch (Figure 111) 1.2 whorls, 0.32 mm, initial 0.75 whorl finely (sometimes strongly) wrinkled, later portion near smooth. Teleoconch whorls highly convex, shoulders well developed, sculpture including well-developed spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, narrowly adnate or slightly disjunct. Inner lip slightly thickened, sometimes forming narrow columellar shelf. Outer lip thin, orthocline to slightly prosocline, sinuate. Umbilicus rimate or shallowly perforate. Periostracum dark tan or brown.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface frilled; outer margin sometimes having weak rim. Attachment scar thick all around.

Radula (Figure 16D–F)  $675 \times 110 \mu\text{m}$ , with 50 rows of teeth. Central tooth  $26 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp long, narrow, daggerlike; basal cusps medium-large. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-4; neck weak; outer wing 180% of cutting edge length. Inner marginal teeth with 27–32 cusps (basal cusp enlarged); cutting edge occupying 34% of length of tooth. Outer marginal teeth with 30–37 cusps; cutting edge occupying 27% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles light to medium brown. Snout medium to dark brown or black. Foot medium to dark brown. Opercular lobe black along inner edge, elsewhere unpigmented to medium grey-black. Neck unpigmented except for scattered black granules to almost uniform black. Pallial roof, visceral coil black, pigment slightly lighter on genital ducts. Penial filament darkly pigmented; pigment granules sometimes also scattered on base.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned well posterior to middle of ctenidium. Renal

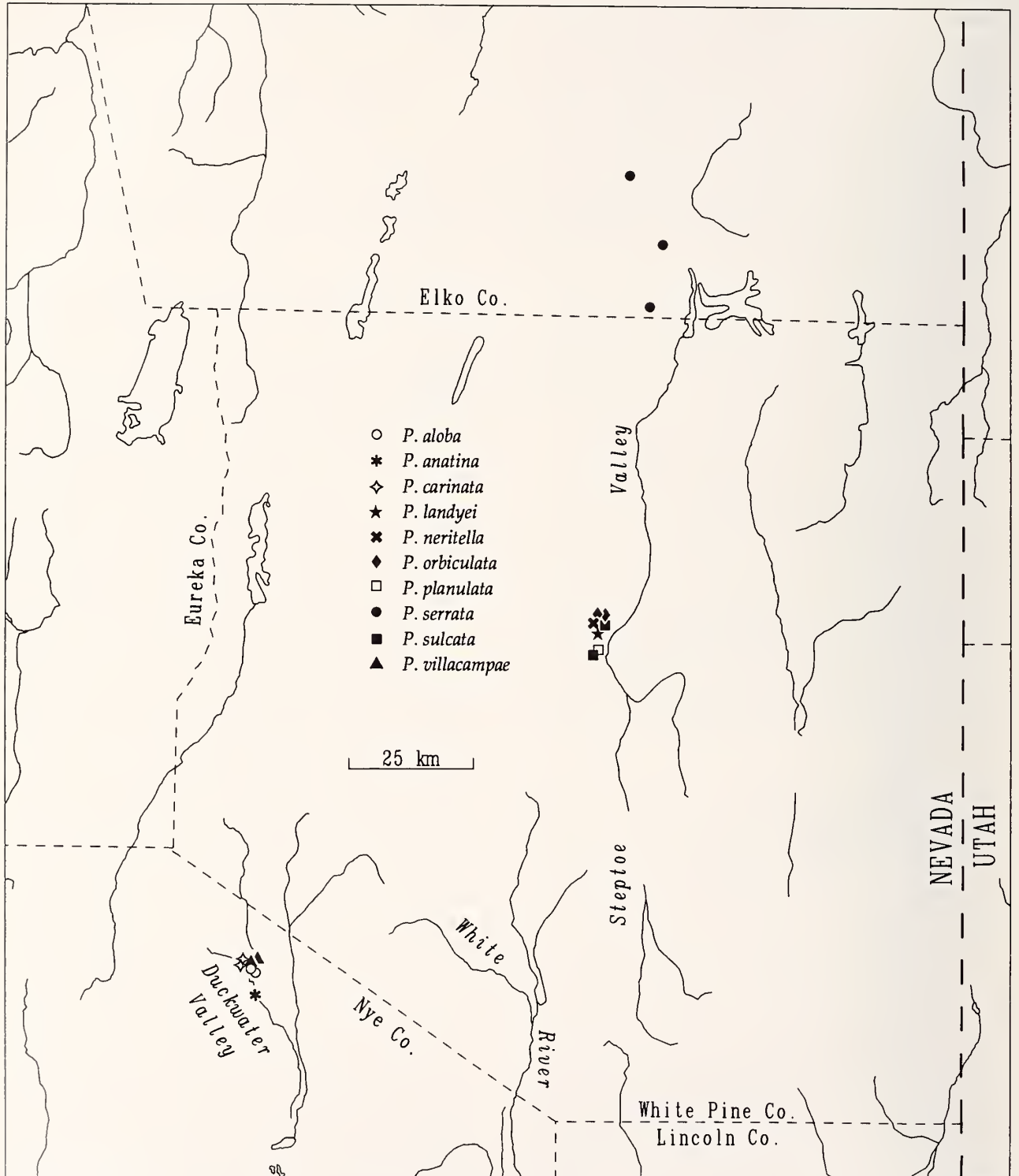


Figure 51

Map showing distributions of locally endemic *Pyrgulopsis* species of Duckwater and Steptoe Valleys, Nevada. In cases where congeners are sympatric, symbols are slightly offset.

gland slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 45G. Albumen gland having short pallial component. Capsule gland sub-equal to albumen gland in length and width, sub-globular in section, rectal furrow well developed. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a sub-terminal pore having short anterior extension. Coiled oviduct a small, posterior-oblique loop preceded and overlapped by weak twist (sometimes forming a similar posterior-oblique loop). Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix short, almost as wide as albumen gland, sub-globular to ovate, longitudinal, with 33–50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 66% of bursa length, medium width. Seminal receptacle small, pouchlike, lateral to proximal portion of bursal duct, positioned near ventral edge of albumen gland.

Testis 1.0–1.25 whorls, filling almost all of digestive gland behind stomach, overlapping posterior and part of anterior stomach chamber. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, often reflexed loop, duct broad. Penis (Figure 45H, I) small to medium-sized; base rectangular, often expanded distally, weakly folded; filament medium length, narrow, often curved, tapering to point, longitudinal; lobe slightly shorter to as long as filament, clublike to hemispherical, longitudinal or slightly oblique. Penial gland large, narrow, slightly raised, positioned along outer edge of proximal filament and distal base. Penial duct straight, near outer edge.

**Type locality:** Prather Springs, Thousand Springs Valley, Elko County, Nevada, T. 40 N, R. 64 E, SE  $\frac{1}{4}$  section 21 (Figure 56). Holotype, USNM 874075 (Figure 24E), collected by P. Hovingh, 18 September 1990; paratypes, USNM 860720. The type locality is a small rheocene moderately impacted by cattle.

**Remarks:** While *P. hovinghi* is similar to the other two species endemic to the Thousand Springs drainage (described below) in some respects, particularly the configuration of the distal female genitalia, these snails are heterogeneous in penial and other features and probably do not compose a clade. *Pyrgulopsis hovinghi* differs from the above in having narrower central cusps on the central radular teeth, and is distinguished from these as well as all other congeners by its unique penial ornament, consisting solely of an elongate Dg1 positioned just behind the penial filament.

**Material examined:** NEVADA. *Elko County:* Prather Springs, USNM 860720, USNM 874075, USNM 874715.

*Pyrgulopsis millenaria* Hershler, sp. nov.

Twentyone Mile pyrg

(Figures 10C, 24F, 46A, B)

**Etymology:** From *millenarius* (Latin), of a thousand; referring to the endemism of this snail in the Thousand Springs Creek drainage, Nevada.

**Diagnosis:** Medium-sized, with ovate-conic shell. Penis small; filament medium length, lobe absent. Penial ornament absent.

**Description:** Shell (Figures 10C, 24F) ovate-conic, width/height, 67–78%; height, 2.4–3.1 mm; width, 1.8–2.3 mm; whorls, 4.0–4.75. Protoconch 1.25 whorls, diameter 0.27 mm, smooth except for very small, finely wrinkled area at apex. Teleoconch whorls medium convexity, weakly shouldered; sculpture including faint spiral striae. Aperture ovate, broadly adnate to very slightly disjunct. Inner lip thin, columellar shelf absent or very narrow. Outer lip thin, orthocline, without sinuation. Umbilicus rimate. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface frilled. Attachment scar thick all around.

Radula 780  $\times$  135  $\mu$ m, with 47 rows of teeth. Central tooth 36  $\mu$ m wide, with weakly indented dorsal edge; lateral cusps, 4–5; central cusp medium width, considerably longer than laterals, daggerlike or rounded; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2-1-2(3, 4); neck weakly flexed; outer wing 170% of cutting edge length. Inner marginal teeth with 19–22 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–31 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or having light brown patch proximally. Snout light to dark brown. Foot unpigmented or light brown. Opercular lobe medium to dark brown along sides; small central zone unpigmented. Neck unpigmented or having scattered grey-brown granules. Pallial roof, visceral coil medium brown-black; pigment not uniform. Penial filament darkly pigmented internally.

Ctenidial filaments, 19; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned well posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 46A. Albumen gland having short or no pallial component. Capsule gland as long and slightly narrower than albumen gland, ovate in section; rectal furrow very weak. Ventral

channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct a posterior-oblique loop sometimes preceded by posterior-oblique twist, coil sometimes kinked or twisted at mid-line. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, positioned along ventral margin of gland, sub-globose to ovate, usually having silvery sheen, longitudinal, with 33% or less of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 66–100% length of bursa, medium width. Seminal receptacle small, narrow pouchlike, overlapping or ventral to anterior half of bursa, sometimes partly overlapped by albumen gland.

Testis 1.5–1.75 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland small, sub-globose, pallial portion very short, narrowly ovate in section. Proximal pallial vas deferens looped. Penis (Figure 46B) small; base rectangular, strongly folded along inner edge; filament medium length, broad, muscular, tapering, longitudinal; lobe absent, distal edge of penis blunt; glands absent. Penial duct straight, near outer edge.

**Type locality:** Springs, below Twentyone Mile Dam, Thousand Springs Creek, Elko County, Nevada, T. 42 N, R. 67 E, SW ¼ section 14 (Figure 56). Holotype, USNM 874720 (Figure 24F), collected by R. Hershler and P. Hovingh, 30 August 1992; paratypes, USNM 860721. The type locality is a small rheocene (Figure 5F).

**Remarks:** *Pyrgulopsis millenaria* differs from other species locally endemic in Thousand Springs drainage in having a much smoother protoconch and bursa copulatrix positioned near the ventral margin of the albumen gland. It is further distinguished from these and other species in the region in consistently lacking both a penial lobe and penial glands. This snail does not closely resemble other Great Basin species that have a simple penis.

**Material examined:** NEVADA. *Elko County:* Springs, below Twentyone Mile Dam (Figure 5F), USNM 860721, USNM 873329, USNM 874720.

*Pyrgulopsis lentiglans* Hershler, sp. nov.

Crittenden pyrg

(Figures 10D, 24G, H, 46C–E)

**Etymology:** From *lentis* (Latin), lentil-shaped; and *glans*, gland; referring to the dotlike terminal gland on the penis of this species.

**Diagnosis:** Small, with ovate-conic to pupiform shell. Penis large, filament medium length, lobe short or absent. Penial ornament a very small terminal gland (often absent).

**Description:** Shell (Figures 10D, 24G, H) ovate-conic to pupiform, width/height, 58–71%; height, 1.4–1.8 mm;

width, 0.9–1.2 mm; whorls, 4.25–4.75. Protoconch 1.2 whorls, diameter 0.27 mm, initial 0.75 whorl finely wrinkled, otherwise smooth. Teleoconch whorls low to medium convexity, without shoulders, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually slightly disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, prosocline, sometimes weakly sinuate. Umbilicus rimate to shallowly perforate. Periostracum tan.

Operculum ovate, amber; nucleus eccentric; dorsal surface strongly frilled; outer margin sometimes having weak rim. Attachment scar strongly thickened between nucleus and inner edge, slightly thickened along inner edge.

Radula  $440 \times 70 \mu\text{m}$ , with 60 rows of teeth. Central tooth  $15 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp medium width, spoon-shaped; basal cusps medium-large, sometimes accompanied by weak thickenings to outside. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3–1–4; neck weakly flexed; outer wing 225% of cutting edge length. Inner marginal teeth with 24–26 cusps; cutting edge occupying 33% of length of tooth. Outer marginal teeth with 26–32 cusps; cutting edge occupying 25% of length of tooth. Stomach as long as style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles unpigmented to medium brown. Snout light to dark brown. Foot light brown. Opercular lobe nearly unpigmented or having light, diffuse, grey pigment all around. Neck unpigmented except for scattered granules to light brown. Pallial roof, visceral coil medium to dark brown, sometimes uniformly pigmented. Penial filament darkly pigmented for almost entire length; base having scattered black granules.

Ctenidial filaments, 15, pleated; ctenidium connected to pericardium by short efferent vein. Osphradium 33% of ctenidium length, narrow, positioned posterior to middle of ctenidium. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure 46C. Albumen gland having medium pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal pore sometimes expanded or mounted on weak papilla; anterior extension absent. Coiled oviduct a posterior-oblique loop, often kinked at mid-length and/or preceded by small posterior twist. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, sub-globular to ovate, often having silvery sheen, longitudinal or slightly oblique (anterior end dorsal), with 50–80% of length posterior to gland. Bursal duct originating from

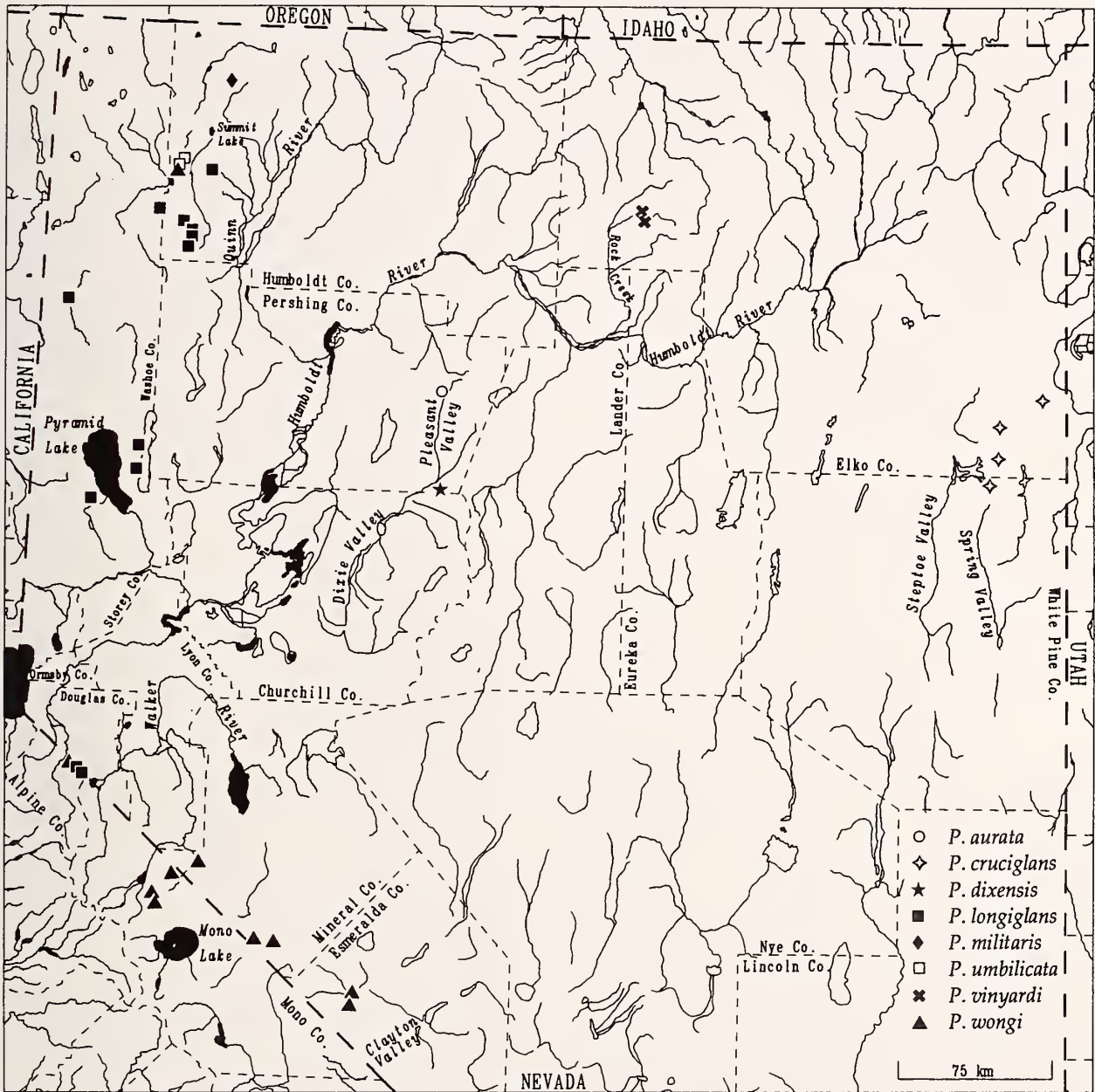


Figure 52

Map showing distributions of *Pyrgulopsis* species of isolated basins of Nevada and the Lahontan Basin. Previously known records for *P. wongi* are not shown. The distributions of *P. limaria* and *P. notidicola*, locally endemic species dwelling in very close proximity to *P. umbilicata* (in Mud Meadows), are not shown.

anterior edge at or near mid-line, slightly shorter to as long as bursa, medium width. Seminal receptacle small, pouchlike, overlapping or lateral to anteriormost bursa or proximal bursal duct.

Testis 1.25–1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and

part of anterior stomach chamber. Prostate gland small, bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens nearly straight or having a weak loop. Penis (Figure 46D, E) large; base rectangular, weakly folded or smooth; filament medium length and width, muscular, tapering to point; lobe short,

pointed, slightly oblique; sometimes nearly absent, with distal edge of penis rounded and slightly bulging. Terminal gland very small (often absent), dotlike, ventral. Penial duct straight, near outer edge.

**Type locality:** Crittenden Springs, Thousand Springs Creek, Elko County, Nevada, T. 42 N, R. 69 E, NE  $\frac{1}{4}$  section 8 (Figure 56). Holotype, USNM 874724 (Figure 24G), collected by R. Hershler and P. Hovingh, 30 August 1992; paratypes, USNM 860722. The type locality is a shallow, broad (30 m) rheocrene flowing down a steep mountainside.

**Remarks:** *Pyrgulopsis lentiglans* differs from other endemic species of Thousand Springs drainage in its smaller size and strongly frilled operculum. This snail differs from these and other congeners of the region in having a small penial lobe bearing a very reduced (often absent) terminal gland.

**Material examined:** NEVADA. *Elko County:* Crittenden Springs, USNM 854639, USNM 860722, USNM 873327, USNM 874724.—Spring, southwest corner of Crittenden Reservoir, Thousand Springs Creek, T. 42 N, R. 69 E, SW  $\frac{1}{4}$  section 17, USNM 854540.

*Pyrgulopsis plicata* Hershler, sp. nov.

Black Canyon pyrg

(Figures 10E, 13F, 24I, J, 46F, G)

**Etymology:** From *plicatus* (Latin), folded; referring to the basally folded penis characterizing this species.

**Diagnosis:** Medium-sized, with broadly to ovate conic shell. Penis medium-large; filament medium length, lobe short. Penial ornament a large Dg1.

**Description:** Shell (Figures 10E, 24I, J) broadly to ovate conic; width/height, 72–85%; height, 2.3–2.9 mm; width, 1.8–2.2 mm; whorls, 4.0–4.5. Protoconch 1.5 whorls, diameter 0.38 mm; initial 0.5–0.75 whorl very weakly wrinkled (mostly near inner edge), otherwise smooth. Teleoconch whorls medium to high convexity; shoulders absent to medium developed; body whorl often slightly disjunct and strongly translated behind the aperture. Aperture large, ovate, usually disjunct. Inner lip thick, without columellar shelf. Outer lip slightly thickened, orthocline or weakly prosocline, without sinuation. Umbilicus rimate to shallowly perforate. Periostracum light tan.

Operculum (Figure 13F) ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface very weakly frilled. Attachment scar thick all around.

Radula  $740 \times 100 \mu\text{m}$ , with 60 rows of teeth. Central tooth  $26 \mu\text{m}$  wide, with medium to highly indented dorsal edge; lateral cusps, 4–7; central cusp broad, daggerlike; basal cusps medium-sized, sometimes accompanied by weak swelling to outside. Basal tongue broad V-shaped, basal sockets medium depth. Lateral tooth formula 3-1-

3(4); neck weakly flexed; outer wing 150% of cutting edge length. Inner marginal teeth with 19–25 cusps; cutting edge occupying 38% of length of tooth. Outer marginal teeth with 24–30 cusps; cutting edge occupying 30% of length of tooth. Stomach longer than style sac; stomach chambers equal-sized; stomach caecum very small.

Cephalic tentacles medium to dark grey-brown or black. Snout light to dark grey-brown. Foot light to medium grey-brown. Opercular lobe black along outer edge; inner edge medium to dark grey-brown. Neck light to medium grey-brown. Pallial roof, visceral coil dark brown or black. Almost entire length of penial filament and distal penis, particularly portion near outer edge, medium to darkly pigmented.

Ctenidial filaments, 17; without pleats; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5 whorl, filling less than 50% of digestive gland behind stomach, abutting posterior edge of stomach. Distal female genitalia shown in Figure 46F. Albumen gland having short or no pallial component. Capsule gland shorter, narrower than albumen gland, broadly ovate in section; rectal furrow weakly developed. Ventral channel slightly overlapping capsule gland; longitudinal fold weakly developed. Genital aperture a terminal pore, slightly raised, having short anterior extension. Coiled oviduct a tight, posterior-oblique loop. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with 50% or less of length posterior to gland. Bursal duct originating from anterior edge at or near mid-line, 50% of length of bursa, narrow to almost as wide as bursa, duct sometimes shallowly embedded in albumen gland. Seminal receptacle small, overlapping or adjacent to anterior portion of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland small, bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having large, well-developed loop, sometimes weakly reflexed. Penis (Figure 46G) medium-large; base elongate-rectangular, proximal portion folded under remaining penis; inner edge folded; filament medium length, narrow or medium width, tapering to point, slightly oblique; lobe short, hemispherical, longitudinal. Dg1 large, narrow, raised; longitudinal (although proximal portion curves slightly across width of penis), borne along outer edge proximally. Penial duct straight, very close to outer edge.

**Type locality:** Spring, Black Canyon, East Fork Sevier River, Garfield County, Utah, T. 32 S, R. 2 W, NW  $\frac{1}{4}$  section 11 (Figure 56). Holotype, USNM 883594 (Figure



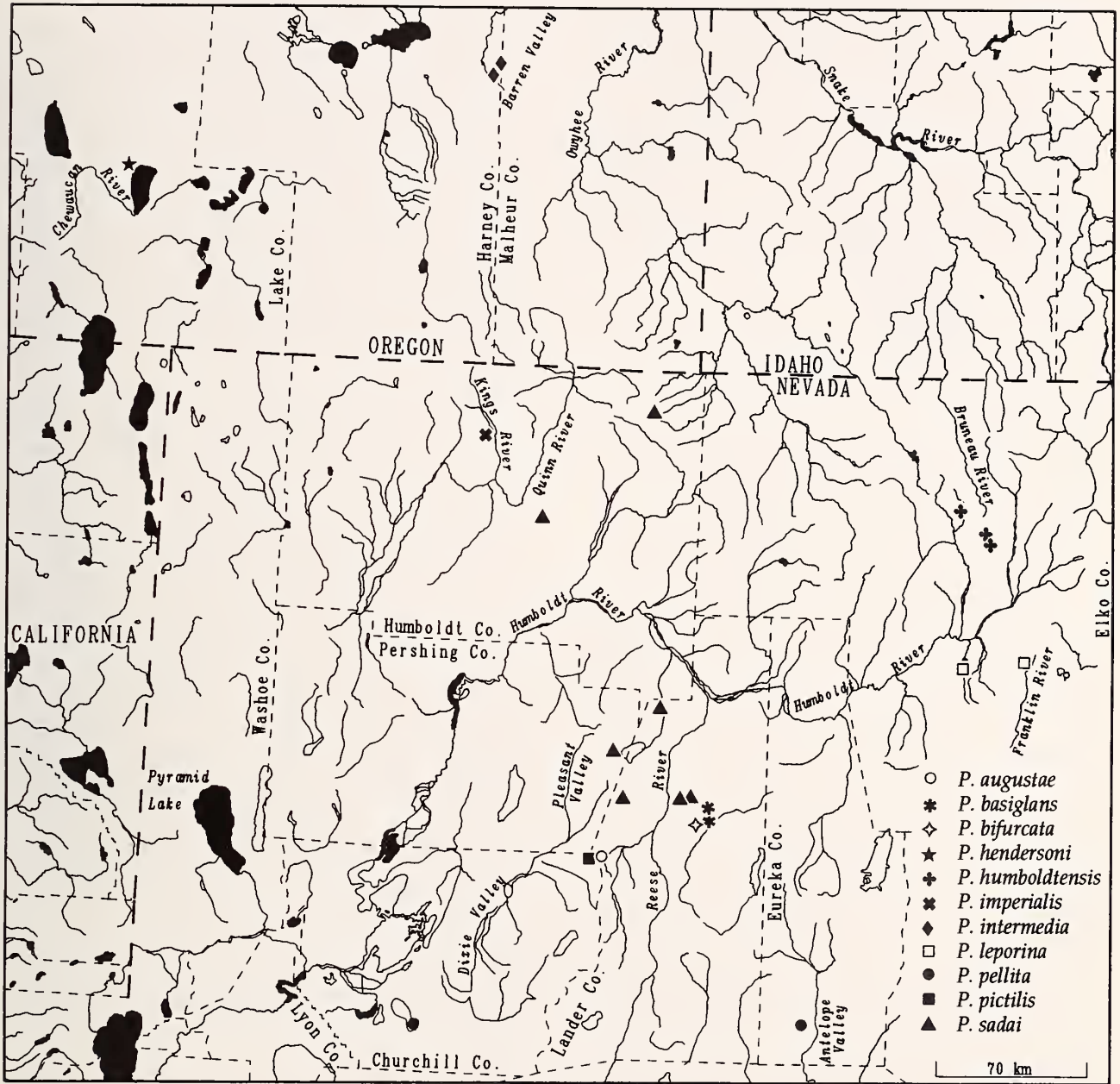


Figure 53

Map showing distributions of *Pyrgulopsis* species of the Lahontan Basin and the Oregon lakes region. Previously known records for *P. hendersoni* and *P. intermedia* are not shown. In cases where congeners are sympatric, symbols are slightly offset.

241), collected by R. Hershler and P. Hovingh, 14 July 1993; paratypes, USNM 860727. The type locality is a series of small rheocrenes emerging from a steep hillside and feeding a reservoir.

**Remarks:** *Pyrgulopsis plicata* differs from other species of the Sevier River drainage in penial ornament, which

consists solely of an elongate Dg1. *Pyrgulopsis cruciglans*, from eastern Nevada, has a similar pattern of ornament, although the gland is much larger and transversely positioned in this species.

**Material examined:** UTAH. *Garfield County*: Spring, Black Canyon, USNM 860727, USNM 883594.

*Pyrgulopsis fusca* Hershler, sp. nov.

Otter Creek pyrg

(Figures 10F, 24K–M, 47A–C)

**Etymology:** From *fuscus* (Latin), dark, swarthy; referring to the black body pigmentation characterizing this snail.

**Diagnosis:** Medium-sized, with ovate- to elongate-conic shell. Penis medium-sized; filament medium length; lobe short. Penial ornament of small terminal, penial, and ventral glands.

**Description:** Shell (Figures 10F, 24K–M) ovate- to elongate-conic, width/height, 61–73%; height, 2.5–4.4 mm; width, 1.6–2.9 mm; whorls, 4.25–5.25. Protoconch 1.5 whorls, diameter 0.40 mm; initial 0.75 whorl very weakly wrinkled (mostly near inner edge), otherwise smooth. Teleoconch whorls medium to high convexity, shoulders narrow to broad, sculpture including faint spiral striae; body whorl often slightly disjunct behind the aperture. Aperture ovate, adnate or slightly disjunct. Inner lip thin, sometimes having very narrow columellar shelf. Outer lip thin, slightly prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum dark tan.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled. Attachment scar slightly thickened along inner edge and between nucleus and inner edge.

Radula  $650 \times 100 \mu\text{m}$ , with 50 rows of teeth. Central tooth  $24 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 3–8; central cusp medium width, spoonlike; basal cusps small, sometimes accompanied by slight thickenings to outside. Basal process V-shaped, basal sockets medium depth. Lateral tooth formula 2(3, 4)-1-3(4, 5); neck weakly flexed; outer wing 220% of cutting edge length. Inner marginal teeth with 21–28 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 27–33 cusps; cutting edge occupying 28% of length of tooth. Stomach slightly longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles dark brown or black, with narrow unpigmented streak centrally. Snout, foot medium brown or black. Opercular lobe sometimes dark along inner edge and/or along outer edge. Neck light to medium grey-brown. Pallial roof, visceral coil dark brown or black. Penial filament darkly pigmented internally.

Ctenidial filaments, 19, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland longitudinal; kidney opening slightly thickened. Rectum broadly overlapping pallial oviduct, slightly overlapping prostate gland.

Ovary 1.0–1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Distal female genitalia shown in Figure

47A. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, sub-circular in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit having short anterior extension. Coiled oviduct usually of two overlapping posterior-oblique loops; proximal loop lightly pigmented internally. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with most of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% to almost as long as bursa, medium width. Seminal receptacle medium-sized, pouch-like, curved or folded, overlapping anteriormost portion of bursa.

Testis 2.0 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland broad bean-shaped, pallial portion short, narrowly ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figure 47B, C) medium sized; base elongate-rectangular, inner edge weakly folded or smooth; filament medium length, broad, tapering to point, longitudinal or slightly oblique; lobe short, truncate, longitudinal. Terminal gland small, sub-circular, distal, ventral. Penial gland small (sometimes reduced or absent), narrower than filament, positioned on filament near base. Ventral gland small, sub-circular or ovate (transverse), borne on low swelling, positioned near base of filament. Penial duct straight, near outer edge.

**Type locality:** Spring brook, Otter Creek, ca. 1.6 km above The Narrows, Piute County, Utah, T. 28 S, R. 1 W, SW  $\frac{1}{4}$  section 17. Holotype, USNM 883439 (Figure 24K), collected by R. Hershler and P. Hovingh, 1 October 1993; paratypes, USNM 860728. The type locality is a small brook (2 cm deep, 1 m wide), fed by numerous small springs, which enters Otter Creek.

**Remarks:** This snail differs from similar *P. kolobensis* in its much narrower penis, with very reduced lobe, and weakly developed glands; and smaller, narrower bursa copulatrix. The distribution of this snail is shown in Figure 56.

**Material examined:** UTAH. *Piute County:* Spring brook, Otter Creek, USNM 860728, USNM 883439, USNM 883484. *Sevier County:* Burr Creek, Otter Creek drainage, T. 25 S, R. 1 W, SW  $\frac{1}{4}$  section 26, USNM 883573, USNM 892028.—Spring, Little Lost Creek, Sevier River drainage, T. 24 S, R. 1 E, center section 18, USNM 883430, USNM 883442.

*Pyrgulopsis chamberlini* Hershler, sp. nov.

Smooth Glenwood pyrg

(Figures 10G, 25A–C, 47D–G)

**Etymology:** Named after the late Ralph V. Chamberlin, in recognition of his extensive fieldwork and taxonomic

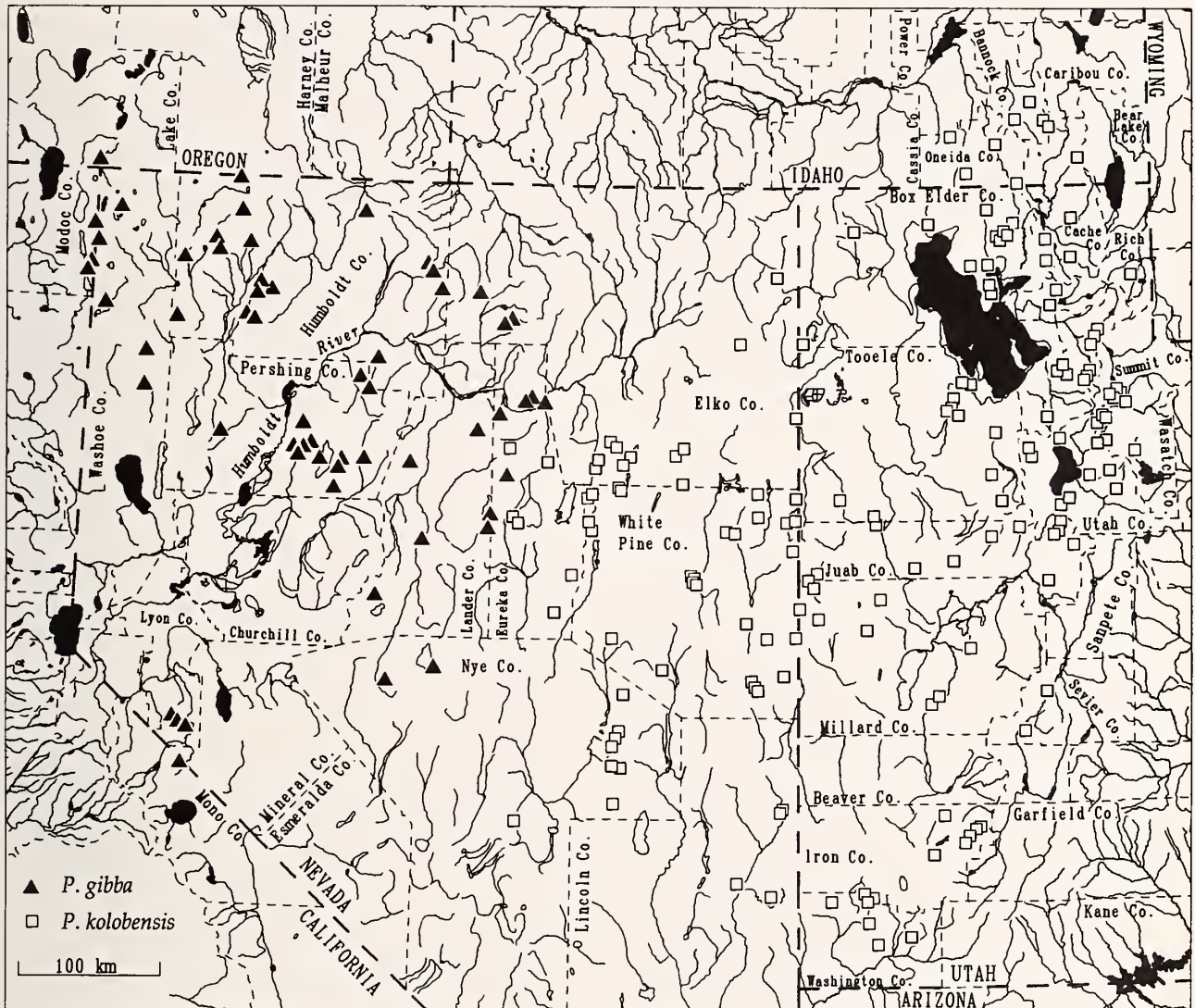


Figure 54

Map showing distributions of *P. gibba* and *P. kolobensis*. Previously known records for *P. gibba* are not shown.

studies pertaining to aquatic mollusks of the eastern Great Basin.

**Diagnosis:** Medium-sized to large, with ovate-conic shell. Penis large, filament medium length, lobe short. Penial ornament a medium-sized terminal gland, large penial gland, large Dg1, small Dg2, small Dg3 (sometimes absent), one to six additional dorsal glands, and small ventral gland.

**Description:** Shell (Figures 10G, 25A–C) ovate-conic, width/height, 64–78%; height, 2.3–4.3 mm; width, 1.8–3.1 mm; whorls, 4.5–6.0. Protoconch 1.25 whorls, diameter 0.33 mm; very weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium convexity,

shoulders well developed, often having with broad shelf; body whorl often slightly disjunct behind the aperture. Aperture ovate, slightly disjunct in largest specimens. Inner lip slightly thickened, columellar shelf medium width. Outer lip usually thin, but slightly thickened in largest specimens, prosocline, without sinuation. Umbilicus absent or narrowly rimate. Periostracum light green.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface weakly frilled. Attachment scar thick all around, broadly so between nucleus and inner edge.

Radula 710 × 100 μm, with 62 rows of teeth. Central tooth 28 μm wide, with highly indented dorsal edge; lateral cusps, 4–6; central cusp narrow (sometimes long),

daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3(4); neck weakly flexed; outer wing 175% of cutting edge length. Inner marginal teeth with 26–30 cusps; cutting edge occupying 40% of length of tooth. Outer marginal teeth with 32–34 cusps; cutting edge occupying 25% of length of tooth. Stomach as long a style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented or light brown; proximal section unpigmented. Snout light to dark grey-brown. Foot light brown. Opercular lobe light grey along inner edge, sometimes all around. Neck very light grey. Pallial roof, visceral coil dark brown or black, sometimes uniformly pigmented. Penial filament darkly pigmented along almost entire length; distal base often similarly pigmented.

Ctenidial filaments, 18, weakly pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling 50% of digestive gland behind stomach, abutting or slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 47D. Albumen gland having medium-large (33% or more) pallial component. Capsule gland shorter, narrower than albumen gland, having distinct pigment patch alongside genital aperture, sub-globose in section; rectal furrow weak. Ventral channel broadly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal pore mounted on small papilla, having short anterior extension. Coiled oviduct of two overlapping, posterior-oblique loops, distal loop having dark pigmented streak. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix long, medium width, lying along ventral margin of gland, ovate, longitudinal, 50–75% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% of length of bursa, medium width. Seminal receptacle small, elongate pouch, rarely folded, overlapping anteriormost portion of bursa.

Testis 1.25 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior stomach chamber. Prostate gland large, elongate bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed, reflexed loop. Penis (Figures 47E–G) large; base rectangular, often elongate, smooth or weakly folded along inner edge, usually constricted proximally; filament medium length, narrow, gently tapering, oblique; lobe short, broadly rounded, longitudinal or slightly oblique. Terminal gland medium-sized, ovate, rarely bifurcate, usually transverse, ventral. Penial gland filling most of length of filament and small portion of base, almost as wide as filament. Dg1 large, narrow, raised on low pedicel, longitudinal (although proximal portion sometimes oblique), borne along outer

edge proximally, rarely abutting the penial gland, sometimes accompanied along inner side by small, circular, raised gland. Dg2 small, ovate, distal. Dg3 small, ovate-elongate (sometimes dotlike or absent), slightly raised. Dorsal surface having one to six additional longitudinal glands proximal to Dg2, units usually dotlike or ovate, but also often including one to two elongate glands near inner edge. Ventral gland small, ovate, transverse, borne on low swelling, positioned near base of lobe; sometimes accompanied by dotlike or small, circular gland proximally. Penial duct straight, near outer edge.

**Type locality:** Spring, Glenwood, Sevier River drainage, Sevier County, Utah, T. 23 S, R. 2 W, NW ¼ section 36 (Figure 56). Holotype, USNM 883576 (Figure 25A), collected by R. Hershler and P. Hovingh, 15 July 1993; paratypes, USNM 860729. Two springs are found in a small drainage at Glenwood. An upper spring flows alongside HWY 119, while in a deeply entrenched area below, a second, more mineralized rheocene emerges amongst a thicket of downed trees. The type locality is the lower spring, which was highly impacted by recreational activities. Note that this species also occurs in the upper spring and that *P. inopinata*, described next, also is present in both springs.

**Remarks:** This species is contrasted above with *P. anguina*, from Snake Valley.

**Material examined:** UTAH. *Sevier County:* Spring (lower), Glenwood, USNM 854786, USNM 860729, USNM 883576, USNM 883944.—Glenwood, FMNH 178389.—Spring (upper), Glenwood, Sevier River drainage, T. 23 S, R. 2 W, NW ¼ section 36, USNM 854784.

*Pyrgulopsis inopinata* Hershler, sp. nov.

Carinate Glenwood pyrg

(Figures 10H, 25D–F, 47H–J)

**Etymology:** From *inopinatus* (Latin), unexpected; referring to the investigator's surprise at discovering a carinate *Pyrgulopsis* along the Wasatch Front.

**Diagnosis:** Medium-sized, with ovate- to narrow-conic shell. Penis medium-sized, filament short, lobe medium length. Penial ornament a medium-sized terminal gland, large Dg1, small Dg2 (often absent), small Dg3, and medium-sized ventral gland.

**Description:** Shell (Figures 10H, 25D–F) ovate- to narrow-conic, width/height, 55–63%; height, 2.9–3.5 mm; width, 1.4–2.1 mm; whorls, 5.0–5.75. Protoconch 1.25 whorls, diameter 0.34 whorls, smooth or very weakly wrinkled at apex. Teleoconch whorls flat to medium convexity, without shoulders, sutures shallow; final 2.0 whorls usually having weak to well-developed peripheral angulation or narrow keel, sculpture sometimes weaker on body whorl; body whorl often slightly disjunct behind

the aperture. Aperture ovate, usually slightly disjunct. Inner lip thickened in larger specimens, without columellar shelf. Outer lip thin, orthocline or slightly prosocline, weakly sinuate. Umbilicus absent or rimate. Periostracum tan.

Operculum ovate, amber, slightly darker in nuclear region; nucleus eccentric; dorsal surface strongly frilled; outer margin having weak rim. Attachment scar strongly thickened all around.

Radula  $610 \times 105 \mu\text{m}$ , with 55 rows of teeth. Central tooth  $29 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 5–7; central cusp medium width, rounded or daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3(4, 5)-1-4(5); neck weakly to medium flexed; outer wing 160% of cutting edge length. Inner marginal teeth with 23–27 cusps; cutting edge occupying 34% of length of tooth. Outer marginal teeth with 28–33 cusps; cutting edge occupying 27% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles medium grey to black, unpigmented around eyes. Snout medium grey to black. Foot light grey to black. Opercular lobe diffuse black along inner edge. Neck light grey. Pallial roof, visceral coil medium grey to black, pigment lighter along genital ducts. Penial filament black along almost entire length; pigment often extending onto distal penis.

Ctenidial filaments, 24, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, positioned slightly posterior to middle of ctenidium. Renal gland longitudinal, kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75–1.0 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 47H. Albumen gland having short pallial component. Capsule gland shorter, slightly narrower than albumen gland, broadly ovate in section; rectal furrow deep. Ventral channel slightly overlapping capsule gland; longitudinal fold small. Genital aperture a terminal pore mounted on a slightly muscular papilla, having short anterior extension. Coiled oviduct of two small, posterior-oblique loops; proximal portion sometimes only weakly kinked. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate, longitudinal, with 50% of length posterior to gland. Bursal duct originating from anterior edge at mid-line, 50% of bursa length, medium width, often shallowly embedded in albumen gland. Seminal receptacle small, pouch-like, overlapping or lateral (ventral) to anterior portion of bursa.

Testis 1.5–2.0 whorls, filling more than 50% of digestive gland behind stomach, overlapping posterior and part of anterior stomach chambers. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal

pallial vas deferens having well-developed, weakly re-flexed loop. Penis (Figure 47I, J) medium-sized; base elongate-rectangular, folded; filament short, narrow, tapering to point, longitudinal; lobe longer (sometimes considerably so) than filament, rectangular, longitudinal. Terminal gland medium-sized, ovate, transverse, largely ventral. Dg1 elongate, extending from middle of penis base near outer edge onto proximal half of filament, almost as wide as filament, slightly raised; longitudinal, but with proximal-most portion slightly oblique. Dg2 small, circular, absent in about 50% of specimens, positioned near inner edge of lobe. Dg3 small, ovate, positioned along outer edge of lobe. Ventral gland medium-sized, ovate, borne on low swelling, transverse-oblique, positioned near base of lobe. Penial duct straight, near outer edge.

**Type locality:** Spring, Glenwood, Sevier River drainage, Sevier County, Utah, T. 23 S, R. 2 W, NW  $\frac{1}{4}$  section 36 (Figure 56). Holotype, USNM 883943 (Figure 25D), collected by R. Hershler and P. Hovingh, 10 May 1995; paratypes, USNM 860730. The type locality is the upper spring at Glenwood (see above), which flows out of a pipe and forms a shallow brook.

**Remarks.** Recent carinate species of *Pyrgulopsis* have previously been recorded only in the western Lahontan and Klamath Lake basins (*P. nevadensis*, *P. archimedis* Berry, 1947, respectively; Taylor, 1960:fig. 1). The penial ornament of *Pyrgulopsis inopinata* is substantially different than that shared by the above species (see Hershler, 1994), as well as that of *P. carinata* from southeastern Nevada (described above), and instead suggests affinity with the group of snails having an elongate, distal Dg1. Among members of this group, *P. inopinata* most closely resembles species from Snake River drainage (*P. robusta*) and Oregon Lakes (*P. hendersoni*), but differs in its smaller size and carinate shell.

At a second, nearby site south of Sigurd, the typical narrow-carinate form of this species is found along with a smooth, ovate-shelled snail. The nature of this variation is as yet unclear—one possibility is that this species may be hybridizing with *P. kolobensis*, which occurs in a typical form in a spring only 3 km to the north.

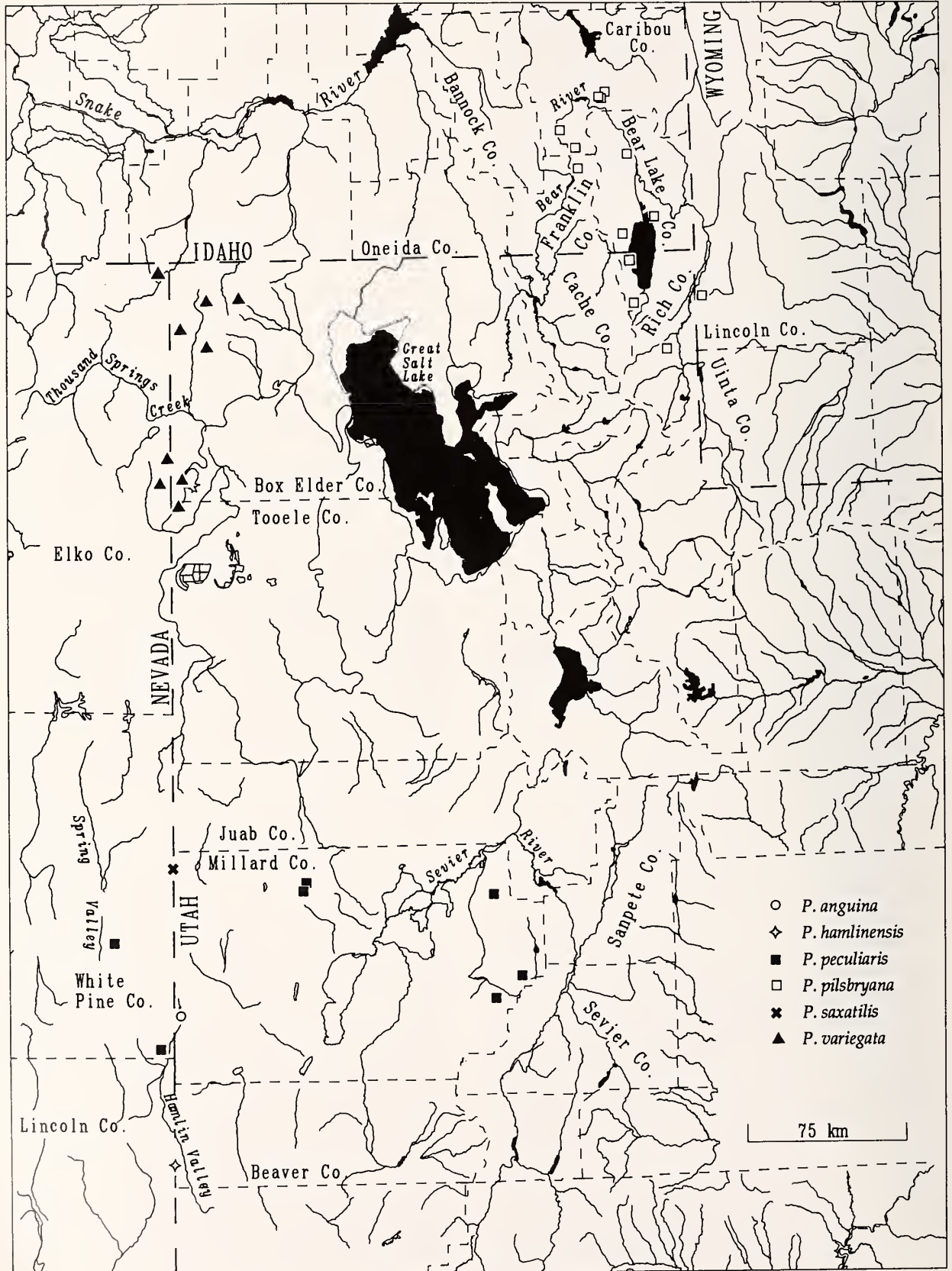
**Material examined:** UTAH. *Sevier County:* Spring (upper), Glenwood, USNM 854783, USNM 860730, USNM 883943.—Spring (lower), Glenwood, USNM 854785, USNM 883886.—Spring, 5.4 km south of Sigurd, Sevier River drainage, T. 23 S, R. 2 W, SW  $\frac{1}{4}$  section 14, USNM 883942, USNM 892032, USNM 892033.

*Pyrgulopsis nonaria* Hershler, sp. nov.

Ninemile pyrg

(Figures 10I, 25G, 48A–C)

**Etymology:** From *nonarius* (Latin), of the ninth; referring to endemism of this species in the vicinity of Ninemile Reservoir, Utah.



**Diagnosis:** Medium-sized, with ovate- to narrow-conic shell. Penis large, filament and lobe short. Penial ornament of large terminal and ventral glands.

**Description:** Shell (Figure 10I, 25G) ovate- to narrow-conic; width/height, 60–71%; height, 2.5–2.9 mm; width, 1.6–1.9 mm; whorls, 4.5–5.0. Protoconch 1.25–1.3 whorls, diameter 0.35 mm; very weakly wrinkled at apex, otherwise smooth. Teleoconch whorls medium convexity, shoulders medium development; body whorl often slightly disjunct behind the aperture. Aperture ovate; usually disjunct. Inner lip slightly thickened, without columellar shelf. Outer lip thin, prosocline. Umbilicus shallowly perforate. Periostracum tan.

Operculum ovate, dark amber; nucleus eccentric; dorsal surface weakly frilled; outer margin having weak rim. Attachment scar thick all around.

Radula  $750 \times 120 \mu\text{m}$ , with 57 rows of teeth. Central tooth  $32 \mu\text{m}$  wide, with medium indented dorsal edge; lateral cusps, 6–7; central cusp broad, daggerlike; basal cusps medium-sized. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 3(4)-1-3(4, 5); neck weakly flexed; outer wing 170% of cutting edge length. Inner marginal teeth with 23–33 cusps; cutting edge occupying 39% of length of tooth. Outer marginal teeth with 29–39 cusps; cutting edge occupying 29% of length of tooth. Stomach as long as style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to dark brown. Snout light to medium brown. Foot unpigmented to light brown. Opercular lobe usually dark brown-black all around. Neck pigmented with scattered grey-brown granules. Pallial roof, visceral coil dark brown-black, pigment often uniform. Penial filament darkly pigmented along most of length.

Ctenidial filaments, 16, pleated; ctenidium overlapping pericardium posteriorly. Osphradium small, narrow, centered well posterior to middle of ctenidium. Renal gland oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.5–0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 48A. Albumen gland having short pallial component. Capsule gland shorter, narrower than albumen gland, subglobose in section; rectal furrow medium depth. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a broad, terminal slit having short anterior extension. Coiled oviduct a pos-

terior-oblique loop sometimes preceded by weak twist or (overlapping) small posterior-oblique coil; coiled portion usually having narrow, light pigment band. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate or sub-globular, longitudinal, with 33–60% of length posterior to gland; anterior portion sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at mid-line, medium length and width. Seminal receptacle medium-sized, pouchlike, overlapping anterior half of bursa.

Testis 1.5 whorls, filling more than 50% of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland bean-shaped, pallial portion short, ovate in section. Proximal pallial vas deferens having well-developed loop. Penis (Figure 48B, C) large; base elongate-rectangular, smooth; filament short, narrow, tapering to point, usually oblique; lobe as long as filament, broad, clublike, longitudinal. Terminal gland large, narrow, slightly curved, transverse, largely ventral. Distal penis bearing two glandular dots (conforming to Dg2) in single specimen. Ventral gland large, narrow, transverse, borne on prominent swelling, positioned near base of lobe, sometimes accompanied distally by small, circular unit (also borne on swelling). Penial duct straight, near outer edge.

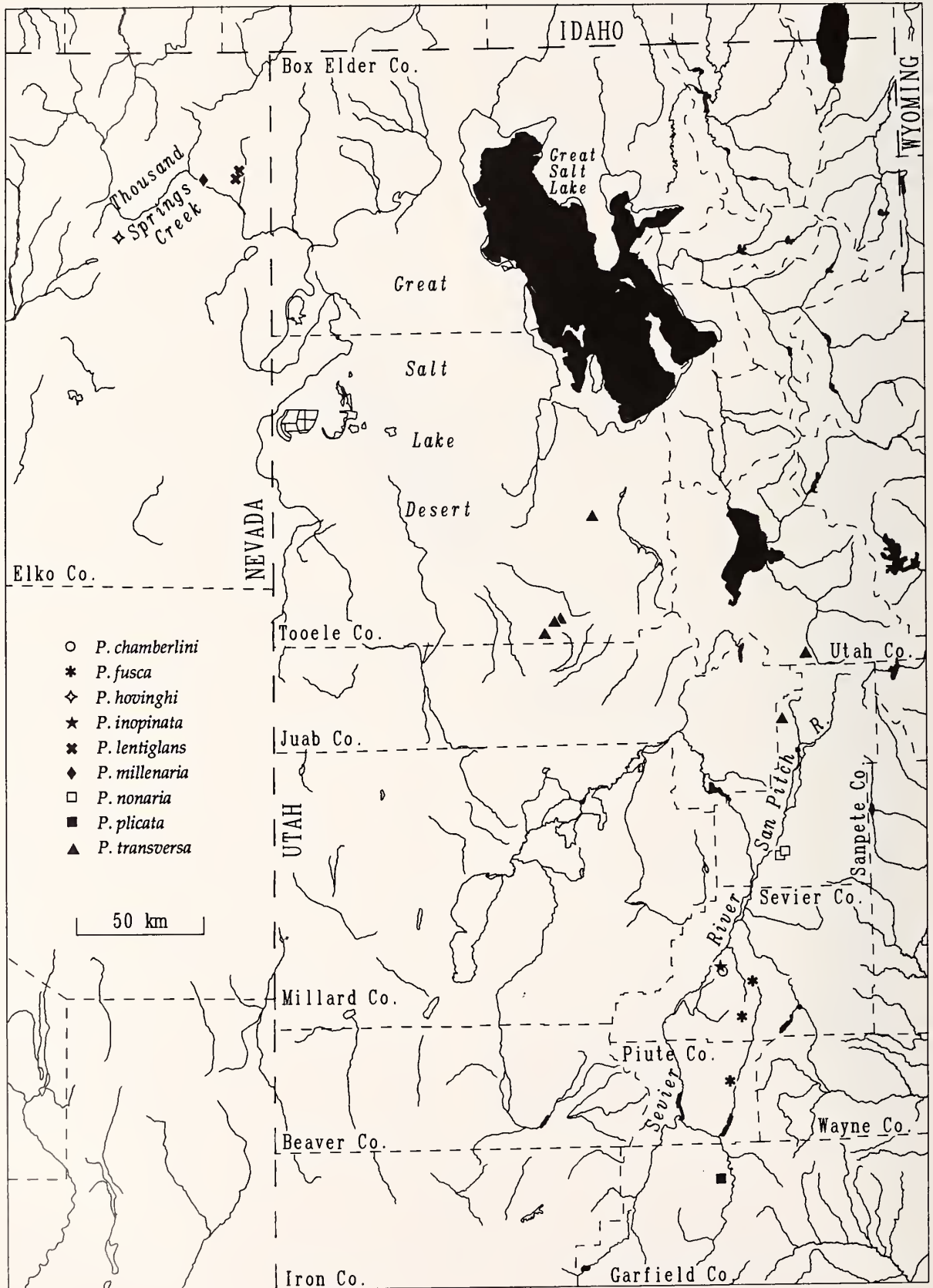
**Type locality:** Spring, east side of Ninemile Reservoir, Sanpete Valley, San Pete County, Utah, T. 19 S, R. 2 E, NW  $\frac{1}{4}$  section 9 (Figure 56). Holotype, USNM 883566 (Figure 25G), collected by R. Hershler and P. Hovingh, 15 July 1993; paratypes, USNM 860731. The type locality is a shallow, broad, mineralized (1213 micromhos/cm) rheocene emptying into Ninemile Reservoir.

**Remarks:** This species is similar to *P. kolobensis* in many details, but differs in consistently lacking a penial gland. Among the group of species having penial ornament consisting solely of terminal and ventral glands, *Pyrgulopsis nonaria* and *P. transversa* (described below), which occurs in the northern portion of SanPete Valley, are distinctive in sharing a relatively narrow shell. These species differ in that *P. nonaria* has a shorter penial filament, larger ventral gland, and a more posteriorly positioned seminal receptacle.

**Material examined:** UTAH. *San Pete County:* Spring, east side of Ninemile Reservoir, USNM 860731, USNM 874376, USNM 883566.—Spring, northeast of Ninemile Reservoir, T. 19 S, R. 2 E, center section 4, USNM 874377.

Figure 55

Map showing distributions of *Pyrgulopsis* species of the Bonneville Basin. Previously known records for *P. pilsbryana* are not shown.





*Pyrgulopsis transversa* Hershler, sp. nov.

Southern Bonneville pyrg

(Figures 10J, 16G–I, 25H–K, 48D–H)

**Etymology:** From *transversus* (Latin), crosswise; referring to the east-west distribution of this species, which cuts across several southern drainages in the Bonneville Basin.

**Diagnosis:** Medium-sized, with ovate- to narrow-conic shell. Penis medium-large, filament and lobe medium length. Penial ornament a small-medium terminal gland and small ventral gland (often absent).

**Description:** Shell (Figures 10J, 25H–K) ovate- to narrow-conic, width/height, 58–78%; height, 2.0–3.1 mm; width, 1.3–2.2 mm; whorls, 4.25–5.25. Protoconch 1.4–1.5 whorls, diameter 0.35 mm; weakly wrinkled along inner edge of initial 0.5 whorl, otherwise smooth. Teleoconch whorls low to medium convexity, shoulders weak to medium; body whorl often slightly disjunct behind the aperture. Aperture ovate, usually disjunct. Inner lip thick, with narrow to medium columellar shelf. Outer lip thin, prosocline, without sinuation. Umbilicus rimate or shallowly perforate. Periostracum tan or light brown.

Operculum ovate, amber, nuclear region reddish; nucleus eccentric; dorsal surface very weakly frilled; outer margin sometimes having very weak rim. Attachment scar sometimes slightly thickened along inner edge and between inner edge and nucleus.

Radula (Figure 16G–I)  $650 \times 110 \mu\text{m}$ , with 53 rows of teeth. Central tooth  $26 \mu\text{m}$  wide, with highly indented dorsal edge; lateral cusps, 4–5; central cusp medium width, daggerlike; basal cusps small. Basal tongue V-shaped, basal sockets medium depth. Lateral tooth formula 2(3)-1-3; neck straight or weakly flexed; outer wing 160% of cutting edge length. Inner marginal teeth with 20–22 cusps; cutting edge occupying 37% of length of tooth. Outer marginal teeth with 28–34 cusps; cutting edge occupying 29% of length of tooth. Stomach longer than style sac; anterior stomach chamber larger than posterior chamber; stomach caecum small.

Cephalic tentacles unpigmented to light grey-brown. Snout unpigmented to medium grey-brown. Foot light to medium grey-brown. Opercular lobe black along inner edge, sometimes all around. Neck having scattered black granules. Pallial roof, visceral coil black, often uniformly pigmented. Penial filament usually lightly pigmented on proximal half; penis occasionally unpigmented.

Ctenidial filaments, 17, weakly pleated; ctenidium

overlapping pericardium posteriorly. Osphradium small, narrow, positioned posteriorly. Renal gland longitudinal or slightly oblique; kidney opening grey-white. Rectum broadly overlapping genital ducts.

Ovary 0.75 whorl, filling less than 50% of digestive gland behind stomach, slightly overlapping posterior stomach chamber. Distal female genitalia shown in Figure 48D. Albumen gland having short or no pallial component. Capsule gland shorter, narrower than albumen gland, ovate in section; rectal furrow weak. Ventral channel slightly overlapping capsule gland; longitudinal fold well developed. Genital aperture a terminal slit, sometimes weakly raised, having short anterior extension. Coiled oviduct usually of two small, overlapping posterior-oblique loops (proximal portion sometimes only twisted or kinked); distal loop usually having narrow band of light epithelial pigment. Oviduct and bursal duct joining a little behind pallial wall. Bursa copulatrix medium length and width, ovate-elongate, longitudinal, with 67–80% of length posterior to gland, anterior portion sometimes slightly overlapped by gland. Bursal duct originating from anterior edge at or slightly lateral to midline, medium length and width. Seminal receptacle small, pouchlike, overlapping proximal bursal duct.

Testis 1.5–2.0 whorls, filling almost all of digestive gland behind stomach, overlapping both stomach chambers. Prostate gland very small, bean-shaped, entirely visceral, narrowly ovate in section. Proximal pallial vas deferens having well-developed bend. Penis (Figure 48E–H) large; base rectangular, smooth; filament medium length and width, gently tapering to point, slightly oblique; lobe medium length, slightly narrower than base, clublike, longitudinal. Terminal gland small-medium, circular-narrow, longitudinal-transverse, ventral. Glandular smear seen on base of filament in single specimen. Similar smear conforming to distal Dg2 seen in single specimen. Ventral gland small, circular-ovate, often absent, borne near base of lobe on low swelling. Penial duct straight, near outer edge.

**Type locality:** Sixmile Springs, Simpson Mountains, Old River Bed, Tooele County, Utah, T. 10 S, R. 8 W, NW  $\frac{1}{4}$  section 33. Holotype, USNM 883221 (Figure 25H), collected by R. Hershler and P. Hovingh, 12 May 1993; paratypes, USNM 860732. The type locality is a series of small, mineralized (1126 micromhos/cm) springs at about 1778 m elevation. The spring sampled is a small “rheocrene” issuing out of a pipe (Figure 3D).

**Remarks:** This species is contrasted with *P. nonaria*

Figure 56

Map showing distributions of *Pyrgulopsis* species of the Bonneville Basin. In cases where congeners are sympatric, symbols are slightly offset.

above. The distribution of this species is shown in Figure 56.

**Material examined:** UTAH. *Sanpete County*: Spring, west-northwest of Fountain Green, San Pete Valley, T. 14 S, R. 2 E, NW ¼ section 2, USNM 873333, USNM 883597. *Tooele County*: Sixmile Springs, Old River Bed (Figure 3D), USNM 860732, USNM 883221.—Indian Springs, Simpson Mountains, Old River Bed, T. 10 S, R. 8 W, NE ¼ section 3, USNM 883422.—Spring, Lee Creek, Government Creek drainage, Dugway Valley, T. 9 S, R. 8 W, SW ¼ section 36, USNM 883481.—Springs, Clove Creek, Rush Valley, T. 5 S, R. 6 W, NW ¼ section 32, USNM 883210. *Utah County*: Spring, Thistle Creek, Utah Lake drainage, T. 11 S, R. 3 E, SW ¼ section 12, USNM 883572.

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